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THE ROLE OF SOIL DROUGHT IN THE DISTRIBUTION OF VEGETATION IN THE NORTHERN ROCKY MOUNTAINS [1]

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INTRODUCTION

In regions of wet winters and dry summers especially, the soil acts as the reservoir supplying water to the plants during the growing season. The amount of growth-water held by the soil is set by the field capacity as the upper limit and the permanent wilting percentage as the lower limit. This growth-water is supplied as rain during the wet season, and where it is not maintained during the dry season by ground water, the supply of growth-water is gradually exhausted. The rate of use and the time of exhaustion depends on such factors as the date of the onset of severe transpiration stress, its daily duration and intensity, and upon the plant cover.

The effect of this soil moisture relation on the distribution of species depends on the plants concerned. It has been shown by Daubenmire (1943) that certain mesophytes (tree seedlings) can withstand dry air, provided there is adequate soil moisture. On the other hand they died after relatively short periods when soil moisture was reduced to the permanent wilting percentage. Annuals may flourish early in the season when the upper layer of the soil is still wet and spend the dry season as seeds. Perennial herbs may either keep in contact with moist subsoil or aestivate. Those seedlings which cannot aestivate, must have sufficiently fast growing root systems to keep ahead of the progressive desiccation or they will be eliminated from areas where soil drought occurs.

Unlike the deciduous forests of southeastern North America and the central grasslands, which receive much of their rainfall during the growing season, parts of western North America receive much or most of their precipitation during the winter months, and the summers may be droughty. These droughty areas will suffer progressive depletion of growth water each summer. It has been shown by Pearson (1931) for San Francisco Mountain, where there is drought in June and September, that in the Piñon-juniper and ponderosa pine zones there is frequently soil drought, which may prevent invasion by other species. In the northern Rocky Mountain region in southeastern Washington it has been shown by Weaver (1915) that soil drought was present in the grasslands to a considerable depth by the end of July. Preliminary work by Daubenmire (1947: 130) also has shown that soil drought occurred in the drier forest associations of northern Idaho.

This paper presents the results of a study of the duration of growth water, during the summer of 1950, in seven associations of northern Idaho and southeastern

[1] This problem was suggested by Dr. R. F. Daubenmire of the State College of Washington, whom the writer wishes to thank for help and advice.

Washington described by Daubenmire.[2] The stands selected were in eastern Whitman County, Washington and Latah County, Idaho.

METHODS

The vegetation

Three stands of each of the following associations were studied. The stands were chosen to be representative of climax or near-climax conditions, preferably with seedlings present to show that conditions for reproduction were satisfactory.

1. *Festuca idahoensis/Symphoricarpos albus association.*[3]—This is a grassland association growing on the loessial hills of eastern Washington (Fig. 1.). It is characterised by the grasses *Festuca idahoensis* and *Agropyron spicatum* and by many forbs, including *Balsamorrhiza sagittata, Geranium viscosissimum* and *Helianthella douglasii.* In the spaces between the dominants is a union of annual plants, including *Collinsia parviflora, Bromus mollis* and *Draba verna.* A sparse shrubby union is present consisting of *Symphoricarpos albus* and *Rosa spaldingii,* which reach a height of only about 2 dm.

2. *Symphoricarpos albus association.*—This association is one of shrubs, principally *Symphoricarpos albus* and *Rosa spaldingii,* which may attain a height of 6 dm (Fig. 1). A herbaceous union is present, characterised by forbs including *Lomatium multifidum* var. *dissectum* and *Helianthella douglasii,* and grasses including *Bromus tectorum.* The association is found in grassland areas as islands (Stands 1 and 2) and on northerly slopes, and intermediately between the *Festuca/Symphoricarpos* and *Pinus/Symphoricarpos* associations (Stand 3).

[2] Forest vegetation of northern Idaho and adjacent Washington. Unpublished manuscript. 1950.

[3] Specimens of the species mentioned are deposited in the Herbarium of the University of British Columbia. The scientific nomenclature follows Harold St. John's "Flora of southeastern Washington and adjacent Idaho." Student's Book Corp. Pullman, Washington. 1937.

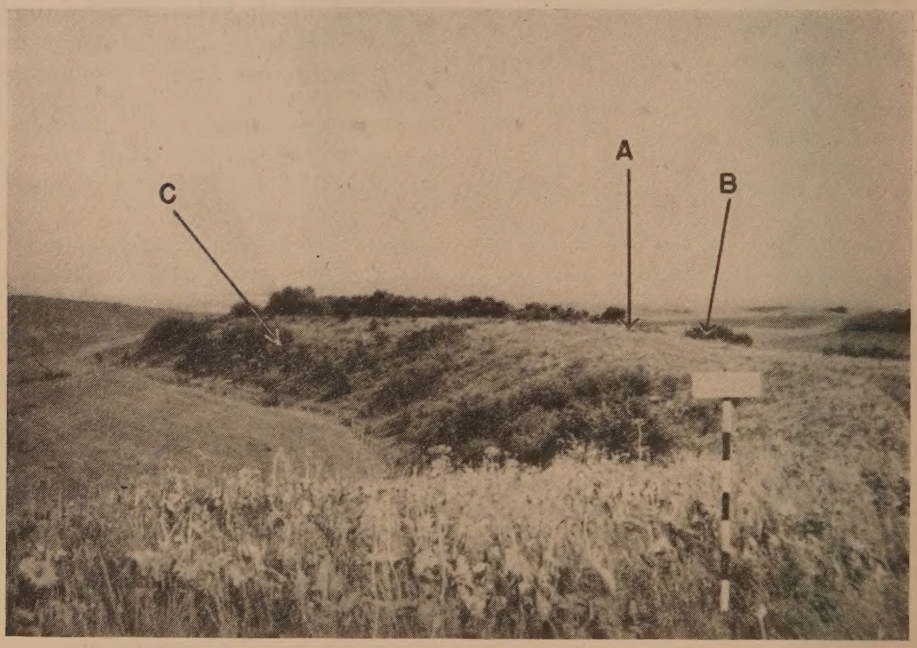

FIG. 1. Stands studied on the prairie relict on the Campus of the State College of Washington; **A** *Festuca/Symphoricarpos,* **B** *Symphoricarpos,* **C** *Crataegus/Symphoricarpos* associations.

FIG. 2. Stand 1 of the *Pinus/Symphoricarpos* association.

3. *Crataegus douglasii/Symphoricarpos albus association.*[4]—On the north slopes of many of the loessial hills thickets of *Crataegus douglasii, Amelanchier alnifolia* and *Prunus virginiana* var. *melanocarpa* form a shrubby union 2 to 3 dm high (Fig. 1). The *Symphoricarpos* union referred to above is also present. The herbaceous union is composed of many species also characteristic of the grasslands, including *Geranium viscosissimum, Gaillardia aristata* and *Gentiana oregona,* and others such as *Agastache urticifolia* characteristic of the association.

4. *Pinus ponderosa/Symphoricarpos albus association.*—The tree union of *Pinus ponderosa* forms a canopy ranging from 20% to 80% cover (Fig. 2). The *Symphoricarpos* union is usually about 5 dm high. The herbaceous union is composed of many of the plants common in the grassland.

5. *Pinus ponderosa/Physocarpus malvaceus association.*—The *Pinus ponderosa* union may be denser than in the previous association. There is a tall shrub union consisting chiefly of *Physocarpus malvaceus, Holodiscus discolor* (Fig. 3), beneath which is the *Symphoricarpos* union. The plants of the herbaceous union are mostly dissimilar to the grassland species, *Osmorhiza* spp., *Trillium petiolatum* and *Thalictrum occidentale* being characteristic.

6. *Pseudotsuga taxifolia/Physocarpus malvaceus association.*—*Pseudotsuga taxifolia* forms the tree union. In many stands, where there has been comparatively recent disturbance, there are a few *Pinus ponderosa,* although there is no reproduction of this species. The other unions of *Physocarpus, Symphoricarpos* and herbs are similar to those in the *Pinus/Physocarpus* association.

7. *Abies grandis/Pachistima myrsinites association.*—*Abies grandis* forms the tree union. The lower union is of shrubs and herbs, many of which are evergreen (Fig.

[4] This name is used provisionally, pending further study of the community.

FIG. 3. Stand 2 of the *Pinus/Physocarpus* association.

FIG. 4. Stand 3 of the *Abies/Pachistima* association.

4). Characteristic species are *Pachistima myrsinites, Coptis occidentalis,* and *Smilacina stellata.*

These associations are part of the altitudinal sequence of vegetation zones found on the west slope of the northern Rocky Mountains. The grasslands are typical of the margins of the basal plains. The pine associations of the foothills are followed by the Douglas fir association, and the Abies association is typical of higher altitudes and wetter regions.

Rainfall

Rainfall records were kept during the period of the investigation to ascertain how much water was added in this form. Table I compares rainfall and air temperature recorded at the Cooperative Station of the U. S. Weather Bureau maintained by the Department of Agronomy, State College of Washington, Pullman during part of 1949 and 1950 with the average for the 55 year period 1893–1948. Although the first three months of 1950 were wetter than usual this was compensated by the drier months of April and May. At Pullman, 7.8 cm of rain was recorded for June. This amount rewet the first two and one half decimeters of the grassland soils, which had fallen below field capacity during April and May when the rainfall had been 2.8 and 2.3 cm respectively. Although the June rainfall was more than usual and may, therefore, have somewhat delayed soil drought, the amount in July and August was quite inadequate to have an appreciable effect on the rate of growth-water exhaustion. For the period July to August inclusive the rainfall in the various stands varied from 1.7 to 3.7 cm. This amount, if applied at one time, is only sufficient to bring 1 to 2 dm of surface soil from permanent wilting percentage to field capacity. Its effectiveness over a two month period would be negligible. The amounts 1.2 and 1.27 cm, the average values for July and August, would be similarly ineffective. Even the record values of 7.3 cm for July 1909 (followed by .02 cm in August) and 6.0 cm for August 1926 (preceded by 0.0 cm in July) would have relatively little influence in altering the pattern of growth-water exhaustion.

TABLE I. *Monthly precipitation and air temperatures for the year beginning October 1949, compared with the 55 year (1893-1948) average, at the Campus of the State College of Washington*

	Precipitation (cm)		Air temperature (°F)					
			Mean Maximum		Mean Minimum		Mean	
	1950	Average	1950	Average	1950	Average	1950	Average
January	10.60	6.65	23.0	34.0	6.1	23.5	14.6	28.7
February	6.60	5.20	37.4	38.0	26.7	25.9	32.1	32.0
March	7.42	5.30	43.5	46.6	31.1	31.5	37.3	39.0
April	2.80	3.72	52.6	56.6	35.3	37.2	44.0	46.9
May	2.38	3.78	62.1	64.4	40.6	43.1	51.4	53.8
June	7.85	3.30	69.2	71.4	49.6	48.6	59.4	60.0
July	.75	1.20	80.7	82.3	54.3	54.1	67.5	68.2
August	.95	1.27	82.1	81.0	53.6	53.4	67.9	67.2
September	2.48	3.20	75.8	70.4	47.0	47.0	61.4	58.7
October	3.91*	4.00	52.2*	58.5	36.8*	39.7	44.5*	49.1
November	5.23*	6.90	52.7*	44.1	38.0*	32.0	45.6*	38.0
December	6.76*	6.75	36.4*	36.4	26.0*	26.2	31.2*	31.3
Total	57.73	51.27						

* 1949

Soil temperature

Soil temperature measurements were made at each of the stands on each of the weekly visits. The records were to

indicate the different temperature regimes under which the seedlings were living and the different temperatures which were affecting evaporation and absorption from the soil. Temperatures were read using a laboratory thermometer placed at 2 dm in a hole first made by plunging in a sharpened steel rod.

Soil moisture

Field moistures were determined by oven drying samples taken by decimetre intervals to a depth of one metre. One metre was chosen as a depth below which seedling roots were unlikely to be able to penetrate in their first season of growth. While the mature plants undoubtedly utilize moisture well below this level, the presence or absence of growth-water in the surface metre of soils plays an important role in seedling survival.

Most of the stands selected were on loess, so that use could be made of a "post-hole" type of borer, a reasonably rapid sampling tool. The number of samples taken at each stand varied from 3 to 4 for each depth in most cases. The stands of each association were sampled once a week during June, July and August. Sampling was done to a sufficient depth to follow the downward progress of exhaustion of growth-water. Comparative tests showed that although at higher moisture levels this number of samples was not entirely adequate to characterise the moisture level of a particular week, it became adequate when the variation decreased as the soils neared permanent wilting percentage. By plotting the moisture against time, for each depth, it was possible to obtain a more accurate picture of water utilization, as weekly sampling errors were smoothed out.

Moisture equivalents, determined by the centrifuge method of Briggs and McLane, were used to indicate the approximate upper limit of the growth water storage capacity. Permanent wilting percentages were determined in the greenhouse using sunflower seedlings (whose leaves indicated wilting) and wheat seedlings (to obtain good root distribution), according to the method described by Daubenmire (1947: 128). In most cases differences among the triplicate replicates were not more than 1%. According to Hendrickson and Veihmeyer (1945), the permanent wilting percentage of a soil may be determined from the field moisture determinations by plotting moisture against time. When the permanent wilting percentage is reached the curve flattens. The beginning of the horizontal part of the curve indicates the attainment of the wilting percentage. This method is probably more reliable than the greenhouse determination, if only for the fact that field conditions are operative, and in the analysis of the data in this paper more emphasis has been placed upon it. It may be noted that in these results the field permanent wilting percentages are usually lower than the greenhouse percentages.

The values obtained for the soil moisture constants, moisture equivalent and permanent wilting percentage, show that there were differences in soil types among the stands. However, as the chief concern of this study was the presence or absence of growth-water, in that depth of soil into which seedling roots might be able to penetrate, other soil characteristics were not considered. Table III shows the moisture equivalents and permanent wilting percentages for the soils of Stand 1 of each association. It may be noted that there are considerable differences in growth-water storage capacity, a factor related to the time of its exhaustion.

RESULTS

Soil temperature

The results for soil temperature are shown in Figure 5. The mean values for the three stands of each association are ploted by months and as a mean for the period of the investigation. The stands were visited at various hours of the day in an attempt to make the time curve of the average hour of visit a straight line parallel to the abscissa. This was achieved

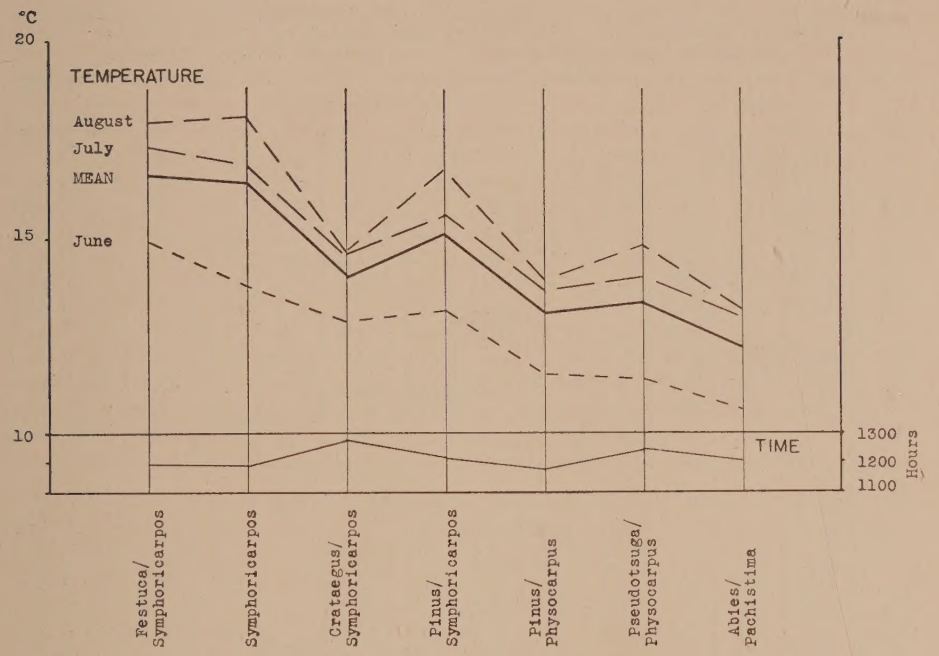

FIG. 5. Soil temperatures at the 2 dm depth for June, July, and August, and mean soil temperatures for the three months combined. The lowest curve shows the average times at which the readings were made. The associations are arranged from left to right in ascending order of normal altitudinal range.

with exception that the *Crataegus/Symphoricarpos* and *Pseudotsuga/Physocarpus* stands were slightly later than the average and the *Pinus/Physocarpus* stands slightly earlier. Table II presents the exposure, slope and altitude of the individual stands. The exposure of some of the stands helps to explain some of the deviations in the curves in Figure 5.

Soil moisture

The data presented in Table III are the mean values obtained from the weekly samplings of Stand 1 of each of the associations. The presence of growth-water may be determined by comparing the individual values with the greenhouse permanent wilting percentages, and with the weekly values according to the suggestion

TABLE II. *Exposure, slope and altitude of stands*

Association	Stand 1			Stand 2			Stand 3		
	Exposure	% slope	Alt. m.	Exposure	% slope	Alt. m.	Exposure	% slope	Alt. m.
Festuca/Symphoricarpos	S	7	800	W	7	760	NW	20	770
Symphoricarpos	W	7	760	S	7	800	E	25	820
Crataegus/Symphoricarpos	NW	40	770	N	50	800	NW	30	760
Pinus/Symphoricarpos	S	35	910	S	8	860	S	15	830
Pinus/Physocarpus	NW	17	880	N	20	850	N	35	830
Pseudotsuga/Physocarpus	S	20	830	N	50	940	S	15	970
Abies/Pachistima	W	40	1250	SW	50	970	NW	15	830

TABLE III. *Soil moisture constants and weekly moisture percentages of the soils of Stand 1 of various plant associations of the northern Rocky Mountains. Values to the left of the step-like lines are considered to be above permanent wilting percentage*

Depth dm	Constants		June		July				August				
	M.E.	P.W.P.											
			Festuca/Symphoricarpos										
1	26.2	13.0	24.0	22.5	14.0	10.6	10.3	7.9	9.3	9.6	8.9	—	9.7
2	26.5	13.0	23.4	—	14.7	12.0	10.7	11.1	10.2	10.2	10.4	—	10.7
3	25.7	12.8	20.8	—	14.7	12.3	11.0	11.8	10.4	10.9	11.1	—	11.7
4	25.8	12.8	14.2	—	—	12.7	11.6	11.6	11.2	11.1	11.7	—	12.0
5	25.8	12.5	14.6	—	—	12.1	11.9	11.4	11.3	11.5	12.1	—	12.0
6	24.3	13.1	15.0	—	—	12.6	11.8	11.6	12.0	11.6	11.8	—	11.8
7	24.5	12.0	15.9	—	—	—	11.8	12.0	11.6	11.5	11.9	12.7	11.6
8	24.2	12.0	16.5	—	—	—	12.0	12.3	11.9	11.5	12.2	11.6	11.8
9	24.6	12.0	18.2	—	—	—	12.5	12.9	12.2	12.2	12.8	11.7	12.1
10	24.9	12.0	18.5	—	—	—	13.2	12.5	12.5	13.0	12.4	12.0	12.4
			Symphoricarpos										
1	31.1	14.0	—	25.1	18.6	15.9	13.0	13.2	—	12.0	12.3	—	12.7
2	28.8	13.3	—	24.9	17.5	15.9	13.7	13.7	—	11.8	12.8	—	12.1
3	27.7	13.5	—	21.9	18.9	15.7	13.3	14.1	—	12.4	12.6	—	11.7
4	27.9	13.0	—	20.7	19.3	16.2	13.1	13.4	—	12.2	12.6	—	11.3
5	26.5	12.5	—	16.2	—	15.8	12.8	13.0	—	11.6	12.6	—	11.8
6	26.1	12.8	—	19.5	—	15.3	13.0	13.8	13.2	11.5	12.4	—	10.9
7	26.7	12.5	—	19.0	—	15.5	13.4	12.5	12.6	11.8	12.0	11.6	11.2
8	26.1	13.8	—	21.0	—	16.6	14.2	12.6	12.2	11.6	12.0	11.3	12.1
9	26.1	12.0	—	20.8	—	16.4	14.7	12.8	12.5	11.6	11.7	11.8	11.2
10	25.3	11.4	—	21.7	—	17.4	13.3	13.6	12.4	11.5	11.5	11.9	11.2
			Crataegus/Symphoricarpos										
1	32.7	14.5	—	22.8	24.3	21.5	15.9	18.0	17.5	14.9	15.7	14.2	16.2
2	29.8	14.0	—	—	24.4	20.2	16.8	16.7	16.0	14.5	14.3	14.7	13.7
3	28.4	12.5	—	—	22.6	—	16.7	15.1	15.4	14.0	14.0	13.7	12.7
4	27.6	12.5	—	—	20.2	—	17.6	14.9	14.0	13.3	13.1	12.8	12.2
5	26.5	12.0	—	—	20.7	—	16.5	15.4	14.6	13.4	12.7	12.7	11.9
6	26.1	11.5	—	—	20.6	—	17.8	15.8	—	13.4	13.3	12.8	12.5
7	25.6	11.5	—	—	21.3	—	17.5	16.4	—	14.0	13.5	—	12.3
8	24.3	11.5	—	—	21.9	—	19.1	16.7	—	13.9	13.0	—	12.2
9	23.8	10.5	—	—	22.3	—	20.4	19.5	—	15.0	13.2	—	12.6
10	24.1	10.5	—	—	23.2	—	20.3	17.5	—	16.4	15.2	—	12.8
			Pinus/Symphoricarpos										
1	17.6	5.0	22.8	20.1	14.5	11.7	9.5	4.9	5.3	4.0	4.9	3.5	3.3
2	15.2	4.8	15.2	—	12.4	10.7	8.9	5.5	4.9	4.3	4.7	3.7	3.3
3	14.5	4.8	14.7	—	—	10.8	8.8	6.8	5.5	4.1	4.7	3.6	3.5
4	15.0	6.5	15.3	—	—	11.3	10.3	7.1	7.1	6.0	5.9	4.7	4.2
5	14.9	6.4	15.4	—	—	12.4	10.8	9.0	7.8	7.3	6.8	5.2	5.5
6	14.6	7.2	18.0	—	—	—	12.5	9.7	—	8.5	8.1	6.7	5.8
7	15.5	6.9	15.4	—	—	—	12.5	10.6	—	9.3	8.5	7.7	6.8
8	13.4	6.4	14.2	—	—	—	13.8	13.7	—	9.6	7.9	7.2	6.2
9	14.5	6.4	14.8	—	—	—	13.8	14.2	—	10.1	10.1	8.1	6.4
10	14.3	6.4	13.6	—	—	—	12.5	12.7	—	9.3	8.9	7.4	6.7

TABLE III. (*Continued*)

Depth dm	Constants		*Pinus/Physocarpus*										
	M.E.	P.W.P.	June		July				August				
1	33.9	14.0	40.0	43.2	29.5	26.3	19.6	14.2	16.1	15.4	13.6	13.6	12.3
2	32.5	12.7	36.8	—	—	24.9	17.9	18.2	14.8	14.8	13.9	13.0	11.8
3	30.2	12.6	36.6	—	—	—	19.1	16.2	13.5	12.8	13.2	11.2	10.8
4	27.3	11.4	33.0	—	—	—	18.0	13.2	12.9	11.8	11.9	10.7	10.5
5	26.8	11.5	30.0	—	—	—	20.0	16.2	14.6	12.4	12.0	10.8	9.8
6	26.0	9.5	29.1	—	—	—	20.4	—	15.5	9.3	9.5	10.7	10.3
7	23.2	9.5	26.1	—	—	—	—	—	11.5	8.6	9.1	9.1	9.4
8	22.9	8.5	22.4	—	—	—	—	—	12.6	9.1	7.8	7.8	8.4
9	21.9	7.5	21.4	—	—	—	—	—	13.6	8.6	7.8	6.3	6.5
10	23.8	8.6	22.8	—	—	—	—	—	11.8	10.3	8.6	8.2	6.2
			Pseudotsuga/Physocarpus										
1	27.3	9.0	—	34.7	23.9	18.9	20.4	11.0	12.3	11.6	9.6	12.1	8.0
2	22.8	7.5	—	—	20.4	16.4	15.0	8.9	9.9	8.5	7.8	9.0	7.1
3	22.4	6.8	—	—	18.3	14.4	11.9	9.2	9.5	8.1	7.4	7.6	7.3
4	19.8	6.1	—	—	18.4	—	12.0	10.2	9.8	8.1	7.4	7.4	6.6
5	20.8	7.5	—	—	17.9	—	13.0	10.6	10.8	9.3	8.0	7.5	7.4
6	19.7	7.8	—	—	17.7	—	15.9	11.2	12.9	9.8	8.7	—	6.5
7	20.5	8.0	—	—	17.8	—	14.0	11.9	12.2	10.5	9.7	—	8.5
8	20.4	9.5	—	—	17.4	—	13.9	12.3	15.3	11.5	10.9	—	11.8
9	23.4	12.0	—	—	19.7	—	17.3	14.9	18.8	15.0	14.6	—	14.3
10	25.1	13.0	—	—	20.0	—	17.5	16.8	17.5	15.3	15.9	—	14.8
			Abies/Pachistima										
1	37.9	13.0	61.3	61.3	46.2	49.1	41.3	34.7	32.1	23.3	22.5	16.8	19.6
2	34.8	13.5	56.9	—	—	—	41.9	34.4	30.8	25.0	23.0	17.7	20.0
3	30.8	13.0	58.0	—	—	—	42.4	37.6	34.0	26.2	22.4	17.1	18.8
4	27.6	12.5	47.1	—	—	—	35.6	36.9	34.4	23.4	17.4	—	17.1
5	26.0	10.0	24.5	—	—	—	21.6	32.4	14.7	13.1	12.1	—	10.4
6	20.1	7.2	19.5	—	—	—	12.5	—	13.3	16.4	12.7	—	10.9
7	16.4	6.0	16.6	—	—	—	—	—	11.6	—	11.2	—	12.2
8	12.7	4.5	21.6	—	—	—	—	—	9.5	—	10.9	—	11.7
9	12.5	4.3	25.9	—	—	—	—	—	—	—	8.9	—	8.7
10	9.9	2.8	24.1	—	—	—	—	—	—	—	7.6	—	—

of Hendrickson and Veihmeyer (1945). Figure 6 shows, for the third decimetre of Stand 1 of the associations, the type of curves that may be obtained by plotting weekly field moisture values against time. The third decimetre is chosen as a level below the normal serious loss of moisture by evaporation, but as one which is sufficiently close to the surface to be critical in the development of seedlings. It can be seen, for example, that the curve for the *Festuca/Symphoricarpos* association flattens before that of the *Pinus/Symphoricarpos* association, while the curve for the *Abies/Pachistima* association did not flatten by the end of August. In Table III the area to the left of the step-like line is considered to have growth-water present, while that to the right represents the absence of growth-water.

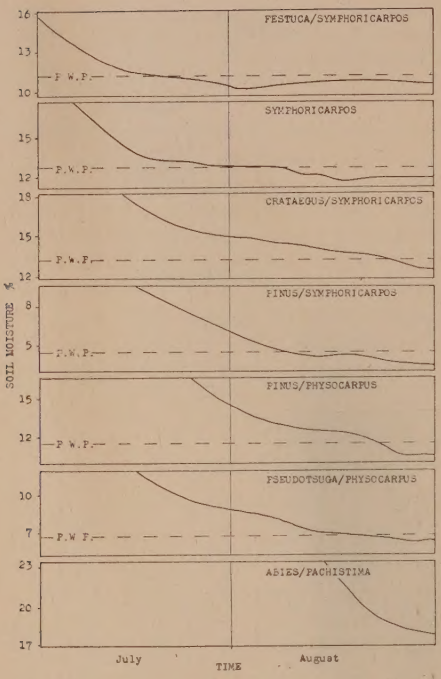

FIG. 6. The variation of soil moisture with time in the third decimetre of Stand 1 of the associations. The horizontal portion of the curves shows that permanent wilting percentage (P.W.P.) has been reached.

Figure 7 shows this relationship for Stands 2 and 3, without giving the numerical basis for the separation of the areas.

DISCUSSION

Soil temperature

It can be seen from Figure 5 that there was a decrease in soil temperature from the *Festuca/Symphoricarpos* to the *Abies/Pachistima* association. There are several reasons why such a temperature gradient occurs. Firstly, the vegetation cover is least dense in the grassland and greatest in the forest. An exception to this is the *Crataegus / Symphoricarpos* association, where the Crataegus canopy in typical cases provides 100% cover, while in the *Pinus/Symphoricarpos* association the tree cover is usually less complete. Secondly, in areas of higher elevation and precipitation, and northerly exposure, the snow cover melts later in the year. Therefore, not only are the soils wetter longer, consequently warming more slowly, but also intense insolation begins later in the season and may last fewer hours per day. The stands of the *Crataegus/Symphoricarpos* and *Pinus/Physocarpus* associations, which are out of place in the temperature series, were all on northerly slopes. This exposure helps to account for their temperatures being lower than those of the associations next above them in the altitudinal sequence (the *Pinus/Symphoricarpos* and *Pseudotsuga/Physocarpus* associations respectively). The soils of the stands of these latter associations were subjected to greater insolation, for they were on more southerly slopes. The soils of the *Pinus/Symphoricarpos* and *Pseudotsuga/Physocarpus* stands also had lower growth-water storage capacities than the *Crataegus/Symphoricarpos* and *Pinus/Physocarpus* stands and were therefore likely to warm more easily. These differences in growth-water storage ca-

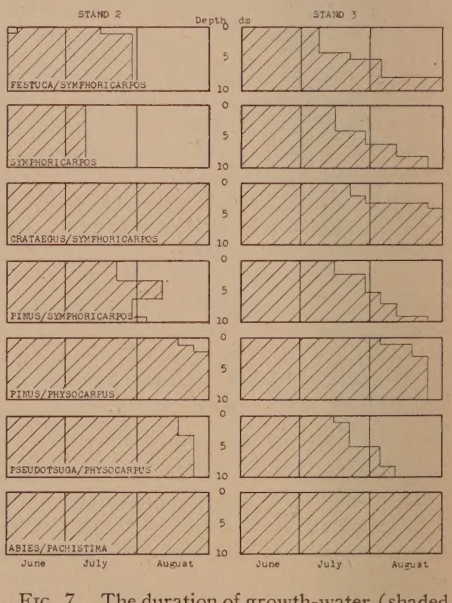

FIG. 7. The duration of growth-water (shaded areas) in the upper metre of the soils of Stands 2 and 3 of the seven associations.

pacities may be attributed to the type of profile developed on the north slopes, where organic and clay contents may be higher, and to slight differences in parent material. The average hour at which the *Pinus/Physocarpus* stands were visited was also earlier than that for the Pseudotsuga stands.

The lower soil temperatures of the denser stands contribute to the improvement in surface soil moisture conditions, for there will be less evaporation and a lower transpiration stress.

Soil moisture

The results in Table III show conditions in stands on typical exposures. It can be seen that the soil drought is earliest and deepest in the grassland and is later in the shrub and forest associations. Figure 7 shows that with different exposures there are variations in the typical depth/time relationships.

Festuca/Symphoricarpos association.—The soil of the upper 5 dm of Stand 1 of the *Festuca/Symphoricarpos* association dried out by mid July. Growth-water was then exhausted to one metre within the next few weeks. It was shown by Weaver (1915) that in fact desiccation may go down 2 m or more. Stand 2 of the association was on a west slope, and was slightly farther east (therefore probably receiving a slightly higher rainfall) than Stand 1, both factors possibly contributing to the later final onset of soil drought. It was the only stand of the association which was sampled prior to the June rains. At that time the first decimetre was already below permanent wilting percentage, which was reflected by the drying up of the *Collinsia parviflora* union. It is probable that Stand 1 was also without growth-water in the first decimetre, for the plants of the *Collinsia* union were equally dry. Stand 3 was at the top of a north slope, which lower down supported a discontinuous stand of the *Symphoricarpos* association. In Stand 3, even by the end of August, the lower levels were not exhausted of growth-water. The plants in the various stands showed this difference in soil water relations, for in Stand 2 they were green several weeks later than in Stand 1, and in Stand 3 later still.

Symphoricarpos association.—The soil of Stand 1 of the *Symphoricarpos* association dried out somewhat later than the adjacent grassland. While still damp this soil was much easier to bore than that of the grassland, probably due to its being extensively burrowed by rodents. Stand 2 dried earlier than the surrounding grassland. However, the looseness of the soil, presumably enabling faster root penetration, may have compensated for this. The root systems of the members of the *Symphoricarpos* union in the shrub association are probably deeper and in more effective contact with growth-water than the plants of the *Festuca/Symphoricarpos* association. Evidence for this is provided by their better growth than the bushes in the latter association and the fact that their leaves remained green more than a month after the grassland herbs had dried. The leaves of the shrubs in Stand 2 remained green longer than in Stand 1 where the soil was less than 2 m deep. Presumably the shrubs can draw upon moisture several metres below ground level. The soil of Stand 3 was more compact than the soil of the other stands, which had been excavated by rodents. The stand was fairly large in extent, on the east end of Kamiak Butte, intermediate between *Festuca/Symphoricarpos* and Pinus stands. The pattern of progressive drought is comparable with the *Pinus/Symphoricarpos* stands studied, reflecting the association's intermediate position.

Pinus / Symphoricarpos association.—Although the exhaustion of growth-water in the *Pinus/Symphoricarpos* stands started only a little later than in the grassland stands, the exhaustion was less abrupt. Its gradual extension would give more chance for the developing pine seedlings to keep ahead of the desiccation. It can also be seen that even by the end of

August drought had hardly extended to 1 m in Stand 1. By the time the rains came in October doubtless soil drought would have gone deeper, but possibly not very much deeper and at a lower rate than it did earlier, for most of the forbs and even some of the Symphoricarpos leaves had begun to dry up by the end of August, thereby decreasing the demand for water. Pine seedlings of several age groups were present in Stand 1, some being of the current years crop. A few of the lower leaves of the latter had dried up, although they may have been killed by the high temperature of the soil surface in this rather open stand. It was observed that such forbs as *Balsamorrhiza sagittata* and *Lupinus sericeus* began to dry about three weeks later in this stand than in the *Festuca/Symphoricarpos* stands, a behaviour paralleling the onset of soil drought in the respective soils.

Stand 2 was on heterogeneous soil, with some parts high in clay and others in coarse material. This made adequate sampling difficult both to find the field value for the permanent wilting percentage and for comparison with the greenhouse values. Only one seedling, about 2 dm high, was recorded, which may be attributable to the abrupt soil drought to a considerable depth. Stand 3 was considerably disturbed by grazing. The absence of seedlings may have been caused by this as well as the early onset of soil drought.

Crataegus/Symphoricarpos association.—The topography and cover of the *Crataegus/Symphoricarpos* stands explain why they had more limited soil drought than the *Pinus/Symphoricarpos* stands. *Crataegus/Symphoricarpos* stands are typical of the northern slopes of loessial hills. These north slopes accumulate many feet of snow in winter. Because they are sheltered from intense insolation the snow lies longer than it does on south slopes, thereby delaying the start of water loss from the soil. The daily duration and intensity of insolation is also less than that of other exposures. The dense cover of the Crataegus stands causes lower temperature and higher humidity than would be the case in the *Symphoricarpos* union under a more open canopy. Water loss from the surface layers of the soil is therefore reduced because of the decreased evaporation rate and transpiration stress to which the subordinate unions are subjected. Another factor is the difference in growth-water storage capacity of the grassland, Crataegus, and Pinus associations soils. In Stand 1 the capacities of the first decimetres were about 13%, 18%, and 12% respectively. The values for the lower layers (12%, 15%, and 10% or less) show the same trend. These facts help to explain why there was only limited soil drought in Stand 1 and none in Stand 2, by the end of August. Stand 3, towards the top of a north slope of the fairly wide valley of Paradise Creek, was more open than the other stands. Although some of the grasses, for example *Poa pratensis,* had started to wither by the end of August, the forb *Gaillardia aristata* was still green when other individuals of the same species in the grassland were already dry.

It is to be noted that soil moisture conditions are more favourable in the *Crataegus/Symphoricarpos* association than in the *Pinus/Symphoricarpos* association and yet pines do not appear to be able to extend down from the foothills and establish themselves naturally on Crataegus habitats. In the stands examined there was no seed source for pines near enough to be effective. However, in those stands near to a seed source it is likely that at least occasionally some of the seed landing in the Crataegus stands would escape the attentions of the apparently high rodent population (judging by the number of burrows and the looseness of the soil). There seem to be two possible explanations why *Pinus ponderosa* is unlikely to survive. It was shown by Pearson (1936) that *Pinus ponderosa* does not survive under conditions of more than 80% shade. Under typically dense *Crataegus/Amelanchier* union shade conditions are likely to be limiting to the sur-

vival of pines. Secondly Haig *et al.* (1941) showed that shade may prevent the survival of seedlings because of the restriction of root growth. In stands of Crataegus, root growth of any pine seedlings may be sufficiently restricted so that even limited soil drought may be fatal. Pines have been established artificially as an erosion control measure, on areas formerly occupied by Crataegus stands, and these are continuing to grow. No seedlings were observed, although this could have been through causes other than drought.

Pinus/Physocarpus association.—In the stands of the *Pinus/Physocarpus* association soil drought started later than in the *Pinus/Symphoricarpos* association. In Stands 1 and 3, however, it extended to more than one metre, which may help to account for the absence of pine seedlings in these stands. Stand 2 was at the foot of a north slope. Only the upper 2 dm had dried by the end of August. Lateral movement of water down the slope, earlier in the season, presumably replenished the growth water. In spite of these improved moisture relations, conditions for reproduction had apparently not been satisfactory in the previous few years for no seedlings were observed. In stands such as these where there were no natural seedlings the survival of seedlings from seed spots would give a good indication of the effect of soil drought.

Physocarpus malvaceus showed fall colouring much earlier in the drier Stands 1 and 3 than in Stand 2.

Pseudotsuga/Physocarpus association.—There were a number of seedlings of Pseudotsuga present in Stand 1 of this association. It can be seen that the soil dried considerably later than in the *Pinus/Symphoricarpos* stands, and that it did not dry so deeply. This probably explains why the slower growing, shorter rooted Pseudotsuga seedlings can become established where soil drought is not extensive. In the pine stands it is apparently extensive enough to exclude Douglas fir. The seedling stages of the members of the *Physocarpus* union can apparently likewise survive some soil drought, but again not as much as the *Symphoricarpos* union.

Although Stand 2 was on a north slope and very wet at the beginning of the season, it dried out fairly suddenly at the end of August. No seedlings were observed in this stand or in Stand 3. Stand 3 was on a south slope. The tree union included several *Pinus ponderosa,* and although there were saplings (1 to 2 m) of both species in an adjacent clearing there were none within the stand investigated. Conditions had apparently been unsuitable for reproduction for several years prior to sampling.

Abies/Pachistima association.—At least until the end of August there was no soil drought in the *Abies/Pachistima* stands. Abies seedlings were common in Stands 1 and 2. Apparently shade conditions imposed by the tree union are sufficient to suppress the less tolerant seedlings of *Pinus ponderosa, Pseudotsuga taxifolia* and of the subordinate *Physocarpus, Symphoricarpos* and herbaceous unions, associated with these tree species. In Stand 3 some of the layers of soil were within one percent of the greenhouse wilting percentages by the end of August, which with the absence of seedlings suggested that conditions in this bottomland stand were not continuously favourable for Abies reproduction.

It was noted that the phenology of the plants which overlapped into the areas occupied by the *Pachistima* union changed. The foliage of both *Arnica cordifolia* and *Frasera fastigiata* had begun drying by mid August in stands with the *Physocarpus* union, but was still green well into September in stands with the *Pachistima* union. Members of the *Collinsia parviflora* union were mostly dry by early June in the grassland, but in the more open parts of the *Abies/Pachistima* stands they were still in flower into July. *Trillium ovatum* was the only plant of the *Pachistima* union to die back during the period of the investigation.

Conclusions

Although the data are for only one season, 1950 did not appear to be abnormal climatically. The results, particularly from the stands in which seedlings were present, show that among the associations there are distinct differences in the amount of soil drought. It seems reasonable to conclude that the absence of growth-water for part of the season apparently prevents survival of those seedlings which cannot endure it by aestivation or evade it by keeping within those horizons in which growth-water is not exhausted. That is, the presence of soil drought prevents the spread of an association into those areas where soil drought is more extensive than its constituent species can endure. A study of soil moisture conditions for several seasons, although it would show differences in extent and timing of soil drought, would probably continue to show similar differences in the amount of drought present among the associations. This factor apparently sets the lower altitudinal limit of range of the associations here considered. Where soil drought does not exclude the species of an association, the boundaries of their distribution may be set by their failure to compete successfully with species of other associations which are more tolerant of shade conditions. The differential action of varying extents of soil drought on seedling survival appears to be one of the most decisive environmental factors controlling the distribution of plant associations on the lower slopes of the northern Rocky Mountains, where summer drought is normal.

Summary

1. An investigation was carried out, during the summer of 1950, on seven plant associations, of grassland, shrub and forest, to ascertain the differences in extent of soil drought and temperature conditions among the various associations. The stands studied were located in Latah County, Idaho and eastern Whitman County, Washington.

2. Rainfall and temperature conditions were similar to the average, although June was rather wetter, so that exhaustion of growth water was possibly later than usual. Rainfall in July and August was so slight that it did not add to the store of moisture in the soil.

3. It was found, with two exceptions, that there was a series, with the grassland soils the warmest and each succeeding association up the slope having progressively cooler soil in summer.

4. It was found that the exhaustion of growth water, from the surface down to one metre or more, by the end of August, in typical stands where seedlings were present, was earliest in the *Festuca/Symphoricarpos* association, later in the *Symphoricarpos* association and last in the *Pinus/Symphoricarpos* association. Soil drought occurred to a limited extent in the *Pseudotsuga/Physocarpus* association and not at all in the *Abies/Pachistima* association.

5. Variations from these typical results occurred with differences in exposure, topography and present condition of the plant cover.

6. The exceptions to the typical sequence were the *Crataegus/Symphoricarpos* association and one stand of the *Pinus/Physocarpus* association, where soil drought was limited in extent and soil temperatures were lower than might be expected from their positions in the altitudinal sequence. Stands of both associations usually occur on northerly slopes, where intense insolation begins later in the season and does not last as long per day as on other exposures. In these cases shade, possibly combined with drought, may limit invasion from other associations characteristic of higher altitudes.

7. The results show that in the region of the northern Rocky Mountains, where precipitation is mostly in the winter and summer drought is normal, different plant associations are correlated with different extents of soil drought.

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RELATIVE ABUNDANCE, HABITATS, AND NORMAL THERMAL LEVELS OF SOME VIRGINIAN SALAMANDERS

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INTRODUCTION

It has been shown that behavioral thermoregulation is characteristic of lizards (Cowles and Bogert 1944) and that virtually identical mean body temperatures are maintained during periods of normal activity by widely separated species belonging to the same genus (Bogert 1949a, 1949b). Studies of local populations show that curves for the "normal activity range" in the body temperatures of individual species are nearly identical, regardless of the season, the locality, or its elevation. Each species has an "eccritic body temperature," actually a zone of "preference," the mean of which is virtually identical for juveniles as well as for adults of either sex. Furthermore, since lizards avail themselves of variations to be found in time and space in the thermal level of their surroundings, it is possible for representatives of distantly related genera to occur side by side and still to maintain significantly different mean body temperatures (Bogert 1949a). Heat derived from the substratum is of some importance, but basking plays a more significant role in their heat economy.

Salamanders, on the other hand, do not bask. Unless they inhabit caves their activities are largely nocturnal. They lack the relatively impermeable skin possessed by most reptiles, and their inability to conserve water further restricts the distributions and the activities of the terrestrial species. They are absent from deserts (where toads exist) and in such semi-arid regions as southern California the few species that occur are nearly impossible to find during the dry season. Drought is commonly accompanied by higher temperatures, but it is probable that seasonal periods of salamander activity are governed by rainfall and humidity cycles rather than by air or substratum temperatures. Shelford (1914) reports that salamanders respond to humidity gradients, whereas Pearse (1909) found that they scarcely reacted, if at all, to thermal gradients.

Frogs respond to low temperatures by seeking a retreat (Torelle 1903), and in temperate zones they emerge from hibernation and breed in a fairly definite sequence of species (Wright 1914; Babcock 1926; Babcock and Hoopes 1940) as air temperatures rise. This information may have been the basis for the statement by Noble (1931, p. 433) that each species "has its own temperature level to which it responds." In the tropics breeding is more often correlated with the advent of the wet season, which may be accompanied by a drop in air temperatures. But some species, the neotropical toad *Bufo marinus* for example, breed during the dry season, possibly as the result of an adaptive specialization that permits them to avail themselves of pools in stream beds that contain swiftly running water during the rainy season. Thus, no definite inference can be drawn concerning the role of thermal factors in the initiation of the breeding season.

Moore (1949a, 1949b) has shown that in the leopard frog, *Rana pipiens,* embryonic tolerances, rate of development, egg size, type of jelly mass, and other characters are closely correlated with the geographic distribution of the local populations studied, and, by inference, represent adaptations to temperature. Unpublished data indicate that toads are sensitive to changes in body temperatures, but thus far it has not been demonstrated that adult amphibians, either frogs, *Rana,* or salamanders, not to mention the caecilians of the tropics, have any definite zone of thermal "preference"

or an eccritic body temperature between the extremes that are tolerated. Neither has it been demonstrated that frogs or salamanders have any ability to discriminate between various thermal levels in their surroundings. However, there is some evidence that adults of various species differ in their temperature tolerances, especially at the upper limit.

Few data concerning body or environmental temperatures of Amphibia in their native habitat have been published. Because of the difficulties in laboratory experiments of distinguishing between the effects of substratum temperatures, air temperatures, and the relative humidity, it seemed worth while to try out field techniques similar to those employed for lizards (Bogert 1949a). If any behavioral control of the body temperature exists in salamanders, curves for series of body temperatures secured for the same species in different localities ought to be similar, as demonstrated for lizards.

The primary purpose of this investigation was to obtain some precise information concerning the temperatures of salamanders in their natural habitats. In order to ascertain whether species differ in their thermal requirements, studies were made of the terrestrial salamanders inhabiting four small areas, two of them in one mountain range, and two of them in another. This procedure permitted us to make comparisons, not only of the data obtained for a few species in each area, but of the data obtained for populations of the same species in separate areas. Comparisons of the relative abundance of species in adjacent areas studied have been included, not only because of their intrinsic interest, but because of the clues such data provide in the interpretation of temperature records.

Acknowledgments

This investigation was carried out during the summer of 1949 at the University of Virginia's Mountain Lake Biological Station. I am grateful to the Director, Bruce D. Reynolds, for facilities placed at my disposal, and for numerous other courtesies. For assistance in the field I am indebted to Vera F. Baron, and to Ernest H. Alderman, Jr., Thomas L. Brooks, 3rd, C. Willard Hart, Jr., Chester A. Mann, James T. Nelson, Jr., Walter Sheppe, Jr., and Paul White, Jr., all of whom cooperated in the project, and assisted in assembling data. Mrs. B. M. Hecht has rendered valuable assistance in making the statistical analyses.

Region

Data presented in this report were obtained in the mountainous region of southwestern Virginia. The first two collections were made in the Balsam Mountains on the southern side of the Roanoke Valley. One collection was assembled on the afternoon and evening of July 7 on and near the summit of Whitetop Mountain between elevations of 5,200 and 5,520 feet, mostly in Smyth and Washington Counties. The following day work was carried on between elevations of 5,200 and 5,720 feet on Mount Rogers in Smyth and Grayson Counties. Both mountains are located in the same ridge, with their summits slightly more than 3.5 miles apart in air line distance.

The summit of Whitetop is covered with a moderately dense stand of red spruce (*Picea rubra*), where *Plethodon metcalfi* was the only salamander encountered. At a level of two hundred feet or so below the highest point on the mountain there is a mixed stand of spruce and deciduous trees along the edge of some small cliffs, where many of the specimens were secured. Here *Desmognathus ochrophaeus carolinensis* and *D. wrighti* occur in essentially the same habitats as *P. melcalfi*. A single specimen of *Eurycea bislineata wilderae* taken under a log is included, although others taken at night in a small stream at the lower level of the area are omitted from tabulations. A few aquatic adults and larvae of other species encountered in this same stream are purposely excluded from this study, as noted below.

Mount Rogers is 200 feet higher than Whitetop, and a few deciduous trees occur along with hemlock at elevations around 5,000 feet. As one ascends Mount Rogers, mixed stands of red spruce and Fraser fir (*Abies fraseri*) are encountered, along with an abundance of rotting logs and stumps, all of them covered with bryophytes. Rocks, beneath which salamanders remain during the day, are frequently encountered at lower elevations, but near the summit they are so completely covered by decaying logs as to be virtually inaccessible to the collector.

The same terrestrial salamanders taken on Whitetop were encountered on Mount Rogers, along with an additional species, *Plethodon welleri*. A few specimens of it were taken between the 5,400 foot level and the summit. *E. b. wilderae*, of which a single individual was secured under a log on Whitetop, was moderately abundant in a restricted area near the highest point on Mount Rogers. One large salamander, probably correctly identified as *Plethodon yonahlossee*, was found under a rock, but it promptly retreated to inaccessible depths; like a few others that escaped capture, it is excluded from tabulations.

Data for two other adjacent populations of salamanders were secured on Salt Pond Mountain in Giles County on the northern side of the Roanoke Valley. The first of these two populations was studied on the afternoon of July 15 in the immediate vicinity of Castle Rock, the highest point along a small escarpment that reaches an elevation of 4,000 feet approximately four miles north of the Mountain Lake Biological Station. After three days of abundant rain, on the afternoon of July 18, a collection for comparison was made within a radius of 250 yards of the Station itself, two collectors being assigned to each of the cardinal directions.

Castle Rock lies on the same ridge, but rises to a slightly higher elevation than that of the Biological Station, which is approximately 3,800 feet above sea level. There is a sharp declivity at the north of Castle Rock, but toward the south there is an irregular slope, at no point very steep. The salamanders obtained in this area were all found along the southern slope of this ridge, within 200 yards of the highest point. The trees in the vicinity are mostly oaks, and there is an abundance of flat rocks, usually two or three inches thick, beneath which salamanders seek refuge. Relatively few logs are present, most of them only partly decomposed. Because of the rocky terrain and the drainage, the vegetation on this ridge is not so dense as it is around the Biological Station, where the land is more nearly level even though a creek traverses the area. Logs were more abundant than rocks as places of seclusion for salamanders near the Biological Station. Here the cover consists largely of deciduous trees, mostly oaks with a few hemlocks, and an undergrowth composed of such shrubs as rhododendrons and mountain laurel.

Plethodon c. cinereus and *P. g. glutinosus* are the only terrestrial salamanders abundant in the immediate region; they are common both at Castle Rock and at the Biological Station. Other species encountered on the days when the survey was made include *Eurycea b. bislineata*, *Desmognathus f. fuscus*, and the terrestrial ("red eft") stage of the newt, *Triturus v. viridescens*. Fourteen salamanders taken at Castle Rock are similar in morphology to *P. c. cinereus*, but lack the red mid-dorsal stripe of the latter and have the dorsum marked with brassy flecks. These have been tentatively identified with the form recently described as *Plethodon huldae* by Grobman (1949) from the Blue Ridge Province.

There is no adequate record of the rainfall at any of the four localities where collections were taken, but inasmuch as work was carried out during the rainy season at a time when rains were of daily occurrence, the terrain in each was extremely moist. Humidity readings were made at intervals with a sling psychrom-

eter, and in forested areas where collections were made, the relative humidity rarely dropped below 90 per cent. Somewhat lower readings could be obtained in cleared areas or in the "balds" on Whitetop Mountain and Mount Rogers, but terrestrial salamanders were uncommon in such places and no collections were made there. Very often the relative humidity approached 100 per cent; even when it was slightly lower where the psychrometer was whirled, the humidity at ground level where the salamanders were located probably approached saturation.

Methods

From some standpoints terrestrial salamanders are ideal for population studies. In the mountains of southwestern Virginia they are comparatively easy to collect. By overturning every log or rock that could be moved at Castle Rock, for example, it was found that ordinarily only five minutes were required to locate, capture, and record data, including the temperatures of the air and substratum, for each salamander. Some species are not ordinarily encountered by overturning logs and rocks. Near the Mountain Lake Biological Station the purple salamander (*Gyrinophilus p. porphyriticus*), for example, could be found only at night along roadside ditches, where it inhabited holes in the bank from which water issued. The holes were of small diameter, usually approximating that of the salamander, and penetrated to depths exceeding two feet. It was thus evident that during the day the salamander remained in seclusion in places where it could not easily be captured. Similarly *Desmognathus quadramaculatus* is restricted to other aquatic habitats, principally creeks or smaller streams, whereas some, like *Eurycea b. bislineata,* may occur in streams or be found under logs on land as well.

The proportion of aquatic salamanders in any sample is, of course, dependent upon the skill of the collector as well as upon other factors inherent in the assemblage of collections from springs, streams or pools. With suitable equipment it would have been possible to capture scores of newts (*Triturus v. viridescens*), and probably no other salamander in the lake a mile south of the Station. Therefore, if populations are to be compared, it is preferable to restrict samples to salamanders from one habitat or the other. Accordingly, all samples utilized in this study consist of collections assembled under conditions as nearly identical as it was feasible to restrict them. Only those salamanders found abroad on land or under rocks, logs, or debris are included, and the collections compared are the results of similar expenditures of time by the same field collectors, all of whom were trained in advance and instructed to collect all specimens encountered.

Temperatures recorded were taken with gas-filled mercury thermometers designed to record temperatures within the range of 0 to 50° C., and calibrated in divisions of 0.2°. The bulb is but 2 mm. in diameter, approximately 12 mm. in length, and thus sufficiently small to absorb heat rapidly enough to permit it to reach equilibrium within 15 seconds when inserted in the soil or a rotten log. Somewhat more time is required for the thermometer to reach equilibrium when air temperatures are taken, even when the instrument is held by the top and the bulb end is waved at the level where one wishes to record the temperature of the atmosphere.

Preliminary experiments indicated that it is impractical to take oral or cloacal temperatures of salamanders. Attempts to hold the animal by a limb or the tail result in twisting movements that separate the animal from the appendage. Moreover, heat from the hand is readily transmitted to the body of the animal. When salamanders are held by the head while the thermometer is thrust into the cloaca, heat from the hands is transferred so rapidly that results obtained are of doubtful accuracy. Despite the greatest

care to avoid the transfer of heat, the mean for the cloacal temperatures of 23 *Plethodon g. glutinosus* proved to be approximately 3° C. higher than that for temperatures of the substratum at the points where each of the salamanders was found. However, when a thermometer was pressed against the skin of a salamander immediately after its discovery, it could be shown that the body temperature of the animal closely approximates that of the moist soil or rotten wood in which it had been secreted; measurable differences did not exceed a fraction of a degree, and could be attributed in most instances to the somewhat unsatisfactory contact with the skin that results when a bulb is pressed against a moist, slippery animal. Air temperatures taken at a distance of 1 or 2 cm. from the ground average about a degree higher than those of the substratum when temperatures are obtained immediately after a rock or log is overturned.

Whereas mean body temperatures of salamanders in diurnal seclusion are found to be virtually identical with mean substratum temperatures, it may be questioned whether data for the latter provide a reliable index to body temperatures of salamanders during their periods of nocturnal activity. In order to ascertain whether differences exist between the mean thermal levels of active and nonactive salamanders, body temperatures of ten *Plethodon g. glutinosus* were obtained from animals found abroad at night. This series of temperatures, obtained by applying a thermometer to the skin, provides a mean of 18.4° C. and a range of 16.0° to 20.3° C. The mean, as well as the extremes, closely approximate those of the temperatures of the substratum beneath inactive salamanders of the same species in the same area. The small differences that exist suggest that the body temperature of an active salamander may fluctuate more when the animal is abroad than it does when the animal has retreated to shelter.

Results

Relative abundance.—By comparing samples, as indexes to the relative abundance of salamanders in various types of terrain, clues concerning the factors involved in the distribution of individual species can be obtained. Samples from two adjacent localities, in each of two regions as described above, are available.

The collections from Whitetop Mountain and Mount Rogers are compared in Figure 1, wherein it may be noted that, with approximately the same number of animals secured at each station, differences between the composition of the two are apparent. *Desmognathus o. carolinensis* and *D. wrighti* appear to be equally abundant, relatively at least, on both mountains, whereas *Plethodon metcalfi*, individuals of which comprise nearly half the Whitetop sample, was scarcely half as

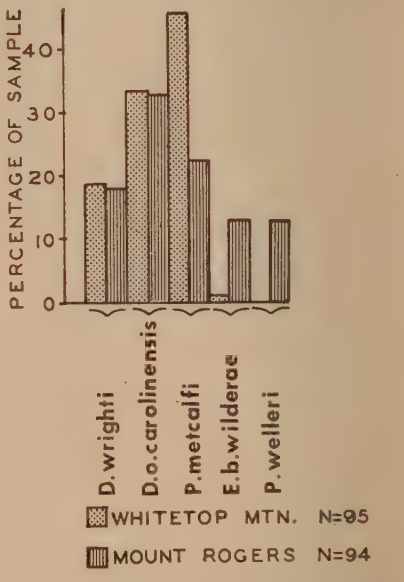

Fig. 1. Bar diagram showing the relative abundance of terrestrial salamanders (*Desmognathus, Plethodon,* and *Eurycea*) in samples obtained on Whitetop Mountain between the elevations of 5,200 and 5,520 feet on July 7, and on Mount Rogers between the elevations of 5,200 and 5,720 feet on July 8. The summits of the two are 3.5 miles apart in the Balsam Mountains of southwestern Virginia.

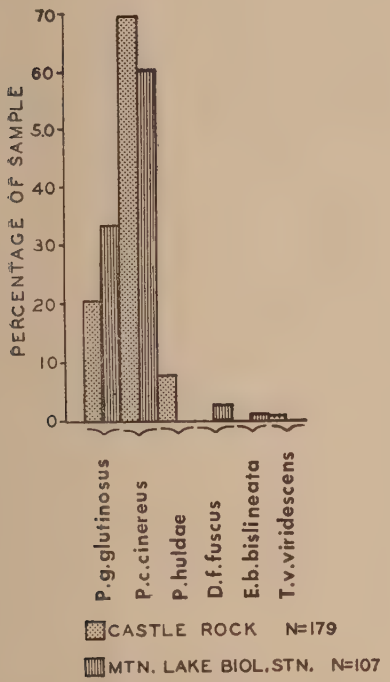

FIG. 2. Bar diagram showing the relative abundance of terrestrial salamanders (*Plethodon, Desmognathus, Eurycea,* and *Triturus* in the red eft stage) at two localities on Salt Pond Mountain in western Virginia in samples obtained on July 15 and 18, respectively, at Castle Rock and the Mountain Lake Biological Station. Castle Rock, a rocky, well-drained area, reaches a maximum elevation of 4,000 feet, 200 feet higher than the Biological Station, which lies four miles to the south in a wetter, more nearly level area.

abundant on Rogers, where two other species, *Plethodon welleri* and *Eurycea bislineata wilderae,* comprise over 25 per cent of the sample.

By virtue of the fact that *P. metcalfi* is a much larger species than *P. welleri* or *E. b. wilderae,* it seems doubtful whether the drop in its relative abundance on Mount Rogers can be ascribed to competition for food. Nor were there obvious differences in the habitat preferences of the three; occasionally individuals of *P. metcalfi* were found in or under the same log with the other two species. Nonetheless, there are differences in the vegetation, in the type of ground cover, and in the mean thermal level of the substratum on the two mountains. Moreover, since the mean and the extremes for substratum temperatures (see below) are lower on Mount Rogers, it may be postulated that minimum temperatures reached on the Mountain are lower than those reached on Whitetop. Thus, any one of these factors in the environment may be less favorable for *P. metcalfi* than it is for the survival of the other two. On the other hand, the similar abundance on the two mountains of the two species of *Desmognathus* would indicate that whatever the factors are that affect the abundance of *P. metcalfi,* they do not affect either species of *Desmognathus,* but favor *P. welleri* and *E. b. wilderae* on Mount Rogers.

Turning now to a comparison (Fig. 2) of population samples taken in the Salt Pond Mountain region, somewhat larger samples are available. However, only two species, *P. c. cinereus* and *P. g. glutinosus,* are actually abundant. Two other species, *Desmognathus fuscus* and *Eurycea b. bislineata,* barely represented in the sample from the Biological Station, were not encountered at Castle Rock only four miles distant. It is probable that they occur there, however. The terrestrial stage of the newt, *Triturus,* represented by one specimen from Castle Rock, was not taken in the collection made at the Station, although it is to be expected throughout most of the area. In contrast, the bronze-flecked form identified as *Plethodon huldae* is not known to occur in the immediate region except at Castle Rock. It may prove to be merely a color phase of the normally red-backed *P. c. cinereus,* which is approximately ten times as abundant as the bronze form at Castle Rock.

It will be noted that *P. c. cinereus* is the most abundant salamander at both localities, although in proportion to the other species in the samples it is ten per cent more abundant at Castle Rock than it is at the Station. If salamanders in-

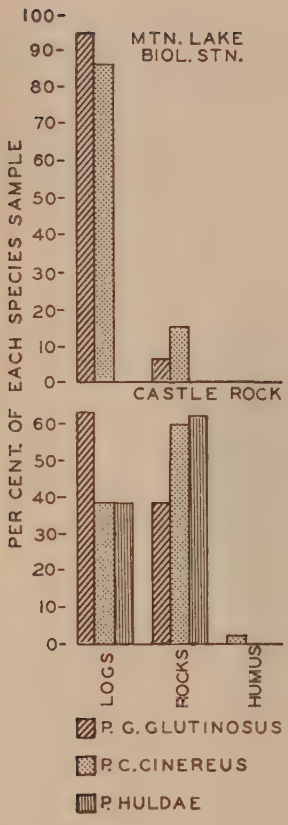

FIG. 3. Bar diagram showing the frequency of occurrence of three species of terrestrial salamanders (*Plethodon*), under logs or rocks or in humus, at two localities, Castle Rock and the Mountain Lake Biological Station on the summit of Salt Pond Mountain in western Virginia. Samples were obtained on July 15 and July 18, respectively.

cluded in the table as *P. huldae* are actually *cinereus,* the species would comprise nearly 80 per cent of the sample taken at Castle Rock.

The larger salamander, *P. g. glutinosus,* comprises slightly more than 20 per cent of the Castle Rock sample, but rises in relative abundance to over 35 per cent in the sample taken but four miles away at the Biological Station. Because of the nearly continuous rains throughout the period when the collections were made, the moisture content of the soil at both places was generally high. Abundant surface moisture at the time the collections were made might be reflected in the size of the samples obtained, but it is less likely that it affects their composition. The size of salamander populations in any area may, of course, fluctuate from time to time. Nonetheless, samples taken should be fairly representative of the inhabitants in each of the two areas during the immediately preceding period.

On the basis of the data it cannot be stated whether *glutinosus* is actually more abundant in one place than it is in the other. It can only be said that, as compared with *cinereus,* it is more abundant at the Biological Station than it is at Castle Rock. This increase in relative abundance can probably be attributed to the greater number of situations at the Station that are moist for prolonged periods in the course of the year. Littleford, Keller, and Phillips (1947) have recently shown that *P. cinereus* can withstand a greater percentage of water loss than *glutinosus.* Noble (1931) comments on the work of Shelford (1914), who studied the effects of evaporation in the two species, and found that responses occurred whether evaporation was due to low humidity, warmth, or movements of the air. Shelford found that *glutinosus* was more sensitive than the smaller *cinereus,* despite the greater surface per unit of weight in the latter. Noble suggests that this may explain why *glutinosus* lives in damper situations than *cinereus.* This inference agrees with our interpretation of the increased relative abundance of *glutinosus* at the Station.

Places of occurrence.—Within the same area the moisture available to a salamander near the surface would vary, not only from time to time, but also from place to place in the microhabitats represented. Depending upon various factors there might be more moisture under a log than under a rock. Or the thigmotropic responses of salamanders may vary from species to species. Also a small sala-

mander like *cinereus,* adults of which are 3 to 4 mm. thick, could readily seek moisture in smaller crevices than could *glutinosus,* mature individuals of which are twice the thickness.

It is of interest, therefore, to attempt some comparisons of the two species in the samples taken at Castle Rock, where rocks were more abundant than logs, and at the Biological Station where the situation was reversed. The data shown graphically in Figure 3 do not include those for the three species that individually comprise less than 3 per cent of the whole sample for each locality. It is pertinent to note that of the 188 salamanders, including the three latter species, for which data were recorded at Castle Rock, 103, or 54.8 per cent were found under rocks, and the remainder under logs, in humus, or on the surface in the open (*Triturus*). At the Biological Station where data were recorded for 107 individuals belonging to four species, only 12 or 11.2 per cent were found under rocks, whereas the remaining 95 (88.8 per cent) were under logs.

Manifestly the place of seclusion is, in part, dependent upon the availability or relative abundance of logs *versus* rocks in each of the areas where collections were made. Figure 3 shows (1) that *P. huldae* and *P. c. cinereus* are represented by almost identical percentages for logs and rocks in the Castle Rock sample (using an adjusted chi-square test, Simpson and Roe 1939, p. 298, $P > .30$; hence, no significant difference is indicated), whereas (2) at each locality higher percentages of *glutinosus* than of *cinereus* are found under logs than under rocks. Using the data for the Castle Rock samples, the difference between the two in this respect is probably significant ($P < .02 > .01$), suggesting that *glutinosus* in that area may differ slightly from *cinereus* in the frequency with which it occurs under rocks when logs are present. But at the Biological Station the slight difference between the two species in the frequency with which they are found under one or the other is not statistically significant ($P > .30$).

In summary, the data obtained indicate that when rocks are more abundant than logs, as is the case in the Castle Rock area, *glutinosus* may occur under logs with slightly greater frequency than *cinereus,* which does not differ in this respect from *huldae.* Inasmuch as *glutinosus* is more sensitive to evaporation, it seems probable that it occurs under logs more often than under rocks because logs tend to retain more moisture.

Thermal levels.—As shown above, *Plethodon glutinosus* in its natural habitat on Salt Pond Mountain seeks shelter under logs slightly more often than rocks, as compared with its smaller congener, *cinereus.* Furthermore, the increase in the

TABLE I. *Substratum temperatures (in °C.) for diurnal shelters of salamanders*

	Castle Rock				Mtn. Lake Biol. Sta.			
	No.	Mean ± σM	Range	V.	No.	Mean ± σM	Range	V.
P. g. glutinosus								
Entire sample	39	18.3±.09	16.8–19.5	3.2	38	17.8±.13	16.4–19.5	4.6
Logs only	24	18.3±.13	16.8–19.5	3.6	36	17.8±.14	16.4–19.5	4.6
Rocks only	15	18.4±.13	17.7–19.4	2.7	2	17.9±.10	17.8–18.0	0.56
P. c. cinereus								
Entire sample	134*	18.5±.05	16.8–20.0	3.1	65	17.9±.11	14.8–19.6	4.7
Logs only	50	18.3±.10	16.8–20.0	4.0	56	17.9±.11	14.8–19.5	4.8
Rocks only	81	18.7±.04	18.0–19.6	1.9	9	18.1±.24	17.0–19.6	4.0
P. huldae								
Entire sample	13	18.4±.18	17.0–19.2	3.6				

* Includes 3 temperature records of salamanders found in humus.

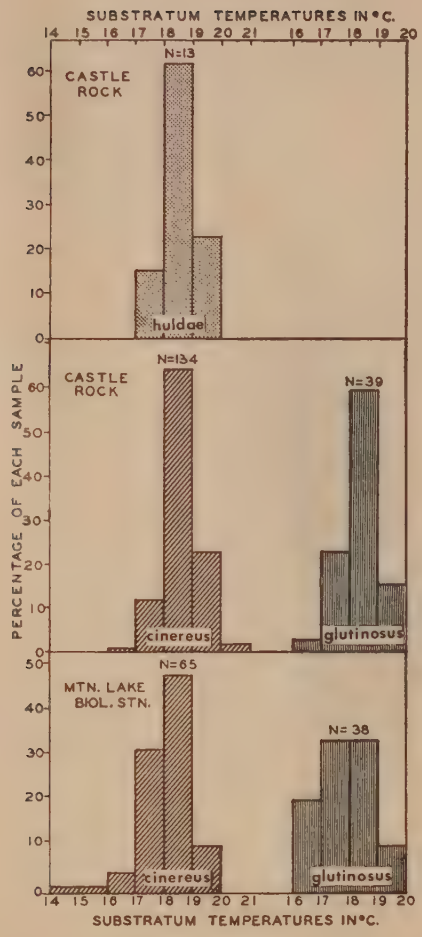

FIG. 4. Histograms indicating the distribution of temperatures of the substratum where terrestrial salamanders of the genus *Plethodon* were found at Castle Rock and the Mountain Lake Biological Station in the Salt Pond Mountain region of western Virginia. Data are plotted between the limits indicated on the abscissa, although actual records were accurate to 0.2° C.

relative abundance of *glutinosus* in the vicinity of the Biological Station, the wetter of the two areas where collections were made, suggests that moisture plays a significant role in regulating the proportional representation of the species. One important question remains to be answered: Is the occurrence of salamanders in one microhabitat or another conditioned by thermal factors? Or in other words, are there significant differences between the species as far as thermal levels of the substratum and body are concerned?

If mean values are compared, it is apparent that the substratum temperatures (Table I) for the two species (Fig. 4) in the same area are similar. The mean for the Castle Rock sample of *glutinosus* is 18.3° C. as compared with 18.5° C. for *cinereus*. At the Biological Station mean substratum temperatures for the two species are, respectively, 17.8° C., and 17.9° C. When the means are compared using the t test formula (Simpson and Roe 1939, p. 211), it can be shown that the differences are not significant ($P > .1$ in both cases). However, when substratum temperatures for *glutinosus* at Castle Rock are compared with those for the same species at the Biological Station, the difference of 0.5° C. between the means is found to be significant ($P < .01$). Moreover, the difference of 0.6° C. between the means for *cinereus* in the two areas is highly significant ($P < .001$).

On the basis of this analysis it is evident that two species inhabiting the same area are virtually identical as far as mean thermal levels of the substratum at the places of seclusion are concerned, whereas both species in the wetter area, with denser vegetation, have significantly lower mean levels.

Plotting of the data in histogram form (Fig. 4) shows that the temperature curves for the *glutinosus* and *cinereus* at Castle Rock are not identical, that for *glutinosus* being skewed toward the lower end of the temperature scale, in contrast to those for both *cinereus* and *huldae*, which are very much alike, and skewed toward the upper end of the scale. Further analysis is desirable, and since the place of seclusion for each individual salamander was recorded, it is possible to compare the temperatures for animals taken under logs with those taken under rocks.

When the means for the substratum temperatures of 24 *glutinosus* found under logs at Castle Rock are compared with those for 50 *cinereus* taken in similar situations in the same area, the minor differences that exist are found to be of no statistical significance ($P > .9$). However, when the mean for the temperatures recorded under rocks for *cinereus* is compared with the mean for *glutinosus* in similar situations, the difference of 0.3° C., small as it is, proves to be statistically significant ($P < .01$). Also, when the mean for *cinereus* under logs at Castle Rock is compared (Fig. 5) with the mean for the same species under rocks in the same area, the difference is found to be highly significant ($P < .001$).

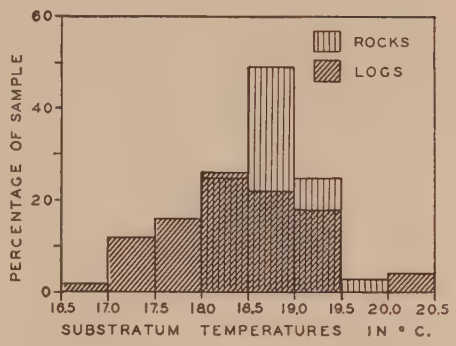

FIG. 5. Histogram showing substratum temperatures for *Plethodon c. cinereus* found under 81 rocks compared with those under 50 logs at Castle Rock. Individual temperatures were recorded for the entire sample within a three-hour period on the afternoon of July 15. Records are plotted between the limits of the individual degrees, without reference to fractions, although temperatures were accurate to 0.2° C.

At Castle Rock a few notes were made of the thickness of the rocks beneath which salamanders were found, and these indicate that *cinereus* occurs more often under rocks three to five centimeters thick, whereas *glutinosus* is more commonly found under rocks two or three times this thickness, and usually also of greater breadth. It is evident from the histogram (Fig. 5) that the temperatures of the substratum under rocks are less variable than under logs, where the thermal level tends to be lower. This may be due to any of several factors, including differences between the indexes of conductivity, the variable penetrability of the abundant moisture from recent rains in logs in various stages of decomposition, or to a number of other factors.

In any event, the fact that more significant differences exist between mean substratum temperatures for *cinereus* found, respectively, under logs and under rocks, than exists between the means for substratum temperatures of the two species in similar situations, suggests that individuals occur where they do because of factors other than the thermal level of the substratum. The slightly higher mean level of substratum temperatures for *cinereus* under rocks as compared with *glutinosus* under rocks may probably be ascribed to greater average thickness (perhaps implying the presence of more moisture) of the rocks beneath which the latter was found. The lack of significant differences between the means (Table I) for either species in the two sorts of retreat at the Biological Station, and the uniformly lower mean levels for salamanders in this area as compared with

TABLE II. *Substratum temperatures (in ° C.) for diurnal shelters of salamanders*

Species	Whitetop Mountain (5,200–5,520 ft. el.)			Mount Rogers (5,200–5,720 ft. el.)			Difference between means
	No.	Mean±σM	Range	No.	Mean±σM	Range	
D. o. carolinensis	31	17.8±.22	16.2–20.1	31	15.5±.18	13.2–17.3	2.3
D. wrighti	4	18.5	17.0–19.8	3	15.7	15.5–15.8	2.8
P. metcalfi	15	18.3±.27	16.4–20.5	21	15.7±.19	13.5–17.4	2.6
P. welleri	0	——	——	10	16.1	15.2–17.1	—
E. b. wilderae	1	18.2	——	4	15.9	15.5–16.6	2.3

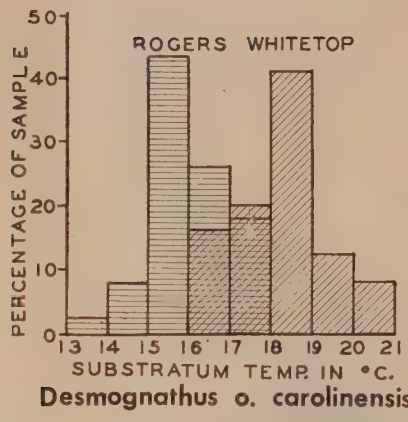

FIG. 6. Histogram comparing substratum temperatures for salamanders of the same species obtained on Mount Rogers between the elevations of 5,200 and 5,720 feet with those obtained on Whitetop Mountain between 5,200 and 5,520 feet. The two samples, each composed of 31 records, were obtained on successive days under similar weather conditions.

Castle Rock suggest that heat is of little importance as an environmental factor influencing the frequency of abundance of salamanders at either site.

Enough data to warrant statistical analyses were obtained in the Balsam Mountains for only two species, *Desmognathus o. carolinensis* and *Plethodon metcalfi*. However, those obtained for all the species collected have been summarized in Table II. Records for the sample representing *D. o. carolinensis* have been plotted in histogram form (Fig. 6).

Despite the inadequacy of the sampling, it is evident that the mean level of the substratum in the diurnal shelters of various species of the salamanders in the same area is approximately the same. However, when data for samples obtained on the two mountains are compared, it is shown that mean substratum temperatures on Mount Rogers average about 2.5° C. lower than those obtained on Whitetop Mountain. On Whitetop the mean for 31 records representing *D. o. carolinensis* is 17.8° C. in contrast to 15.5° C. for the series from Mount Rogers. The difference of 2.3° C. between the means is found to be highly significant ($P < .001$). Calculations reveal an equally significant difference (2.6° C.) between the means for the smaller series of records for *P. metcalfi* on the two mountains.

It is evident from these data that salamanders do not have any marked "zone of preference" as far as body temperatures are concerned. Conceivably they might avail themselves of different thermal levels in their surroundings to maintain the body at a mean temperature characteristic of the individual species, as lizards do. However, there is no evidence that one species of terrestrial salamander differs from another inhabiting the same area as far as the temperature of its microhabitat is concerned. Furthermore, salamanders of the same species that inhabit adjacent mountain tops may live under colder conditions on one than they do on the other.

Discussion

The data presented above show that terrestrial salamanders are found in surroundings where temperatures vary from 13.2° to 20.0° C., most of the records falling within more restricted limits. Test and Bingham (1948) report temperatures beneath logs inhabited by *Plethodon cinereus* in Michigan during May and June to vary from 9.5° to 17.5° and on the litter surface from 7° to 20° C. The minimum temperatures are slightly lower than any encountered in Virginia, where studies were made later in the season.

Stebbins and Riemer (1950) report finding the type specimen of *Plethodon neomexicanus* in a log with a temperature of 12.8° C. in New Mexico. Dr. Stebbins has generously permitted me to summarize some of the unpublished data he has assembled for salamanders in the western portion of the United States. A Mount Lyell salamander, *Hydromantes platycephalus,* found under a rock in a trickle of water at an elevation of 10,800 feet in Tuolomne County, California, had a body temperature of 7.1° C. For three

species of *Batrachoseps* he records substratum temperatures of 10.2° to 10.5° C. for *attenuatus,* and 11.0° C. for *pacificus,* both in Los Angeles County, California; a specimen of *wrighti* taken in Clackamas County, Oregon, was in rotten wood at a temperature of 8.0° C.

He also recorded substratum temperatures for several species of *Plethodon,* including *P. dunni* (7.6° for one in water-soaked soil, and 10.9° C. for water inhabited by others, in Oregon). *P. v. vandykei* (in water at 5.7° C.) in Washington, *P. v. idahoensis* (6.0° C., for soil in rock slide inhabited by 26 individuals), in Idaho, and *P. vehiculum* (11.5° C., under bark) in Washington.

Dr. Stebbins recorded 19.0° C. as the temperature of the water in a reservoir where larval *Ambystoma tigrinum ? nebulosa* were living in Utah; others were in shallow water at 28.2° C. near Pinetop, Arizona. A specimen of *Dicamptodon ensatus* taken under a board in Humboldt County, California, had a body temperature of 9.6° C. He found the aquatic ambystomid, *Rhyacotriton olympicus,* living in water at the somewhat lower temperature of 8.0° C., in both Oregon and Washington.

Newts (*Triturus*) as well as ambystomids can probably tolerate somewhat higher temperatures, both as larvae and as adults. This is in keeping with their occurrence in pools, rather than in mountain brooks, which are more characteristic of aquatic phethodontids. During July a stream with a mean temperature of 13.3° C. near the Mountain Lake Biological Station was inhabited by *Desmognathus q. quadramaculatus, Pseudotriton r. ruber, Eurycea b. bislineata,* and *Gyrinophilus p. porphyriticus.* The same species were taken in streams or springs that varied from 10° to 17.7° C.

Salamanders inhabiting lakes, notably *Necturus,* some newts, *Triturus, Eurycea,* and others, may remain active below the ice throughout the winter months, presumably at temperatures near zero on the Centigrade scale. Noble (*op. cit.*) states that *Necturus* undergoes "an annual migration to warmer waters." Actually it may be inferred that migratory movements represent an avoidance of warmer waters. Mr. Max K. Hecht advises me that it is extremely difficult to capture *Necturus* during the warmer months, apparently because these perennibranch salamanders seek the cooler depths of the lakes or slow moving streams they normally inhabit. *Necturus* is easily caught around the margins of Cayuga Lake during the winter months, but during the summer only larvae—no adults—are taken in shallow water.

As the result of experiments Sayle (1916) concluded that "*Necturus* could not live successfully in water above 18° C.," although no effort was made to control the oxygen content of the water. When dealing with aquatic salamanders it is difficult to distinguish between the effects of high temperatures and the reduction in the oxygen content of the water that results from raising its thermal level. Adult ambystomids and newts (*Triturus*) may tolerate higher temperatures in the water than the lungless plethodontids, principally because their oxygen requirements can, if necessary, be met by taking air into the lungs.

Aquatic larvae may tolerate higher temperatures or other factors may be involved. It has long been recognized (Noble, *op. cit.,* p. 49; Bishop 1943, p. 11) that the cutaneous respiratory apparatus of larval salamanders is adaptively modified. Those living in quiet waters tend to have fins on the back as well as the tail, and to have large bushy gills. The larvae of species that live under conditions where the water is cool, well oxygenated, and running, as it usually is in mountain streams, ordinarily have the fin restricted to the tail and the gills are short. Manifestly the maximum possibilities for cutaneous respiration are provided in cool streams. Larvae that seemingly tolerate higher temperatures, virtually always in quiet water, may actually be able to survive under such con-

ditions only because of their more specialized respiratory mechanisms.

Although embryonic temperature tolerances have been studied intensively in frogs, especially by Moore (1949a, 1949b), who has summarized earlier studies, few precise data are available for salamanders. Bishop (1941) includes a wealth of information concerning breeding habits, but nowhere does he mention the temperature of the water or substratum where developing eggs were found. Gordon and Smith (1949) report an average temperature of 18° C. at the sites where the eggs of the terrestrial salamander *Aneides aeneus* were found in the mountains of North Carolina. Near Castle Rock we found two clutches of the eggs of *Plethodon c. cinereus* with the female coiled around them on June 15, one beneath a rock on a substratum with a temperature of 17.8° C., and a second one under a log at 17.9° C. Several egg clusters of *Eurycea b. bislineata* were found on the underside of rocks in a running stream with a temperature of 10° C. one mile east of the Mountain Lake Biological Station on June 21.

It is manifest that most larval salamanders live under virtually the same thermal conditions as the adults, and it may be doubted whether any significant differences exist between the tolerances of various stages of the same species in any individual population. Exceptions may be found. Adults of *Typhlotriton* are restricted to caves, although the larvae sometimes occur in streams issuing from them. Noble (*op. cit.*) suggests that this may be due to the inability of adults to tolerate the higher temperatures that occur outside the caves. The presence of larval *Necturus* in shallow water after the adults have retreated suggests that the larvae of this form tolerate somewhat higher temperatures.

The information thus far available indicates that body temperatures of terrestrial salamanders during the season of their activity rarely fall below 7° C. or rise much beyond 20° C. There may be differences between species in their toleration of higher temperatures, but there is no indication that salamanders exercise any control over their body temperatures. Consequently differences between species as far as mean body temperatures are concerned are not to be expected. High temperatures may be avoided, and it is not improbable that terrestrial salamanders respond to low temperatures by seeking a retreat, as reported by Torelle (1903) for frogs.

There are too few precise data to permit reliable conclusions, but it seems probable that, as a rule, salamanders live under cooler conditions than the majority of tailless amphibians. Unpublished data indicate that some of the Salientia exercise control over the temperature of the body, and it should be emphasized that conclusions drawn from studies of salamanders are not applicable to the Amphibia as a whole.

Summary

In an effort to ascertain whether terrestrial salamanders exercise any control over their body temperatures, field studies concerned with the relative abundance, habitats, and thermal levels of the common salamanders were carried out on Salt Pond Mountain, and in the Balsam Mountains of western Virginia. Data obtained for the more abundant species may be summarized as follows:

1. Samples of similar size obtained on and near the summits of Whitetop Mountain (elevation 5,520 feet) and Mount Rogers (5,720 feet), which are but 3.5 miles apart in the Balsam Mountains, indicated that two species, *Desmognathus ochrophaeus carolinensis* and *D. wrighti*, are equally abundant in the two areas. On the other hand, *Plethodon metcalfi*, which comprised 45.7 per cent of the sample on Whitetop, represented but 22.1 per cent of the sample obtained on Mount Rogers, the higher of the two mountains. Two other species, *Plethodon welleri* and *Eurycea bislineata wilderae* were uncommon or absent from the sample obtained

on Whitetop, but represented, respectively, by 12.6 and 13.7 per cent of the sample from Mount Rogers. The shift in relative abundance may be ascribed to any of several factors, possibly to differentials in temperature tolerances, although proof for such an assumption is lacking.

When a sample representing a salamander population in the area in the immediate vicinity of the Mountain Lake Biological Station (elevation 3,800 feet) was compared with one obtained in a somewhat drier locality at Castle Rock (elevation 4,000 feet) four miles distant, it was found that *Plethodon c. cinereus* was relatively more abundant in the drier of the two localities. Second in abundance was the larger species, *P. g. glutinosus*. This salamander comprised 21.2 per cent of the sample from Castle Rock, in contrast to 35.5 per cent of the sample obtained in the wetter area near the Station. Although both areas were extremely moist at the time samples were obtained, the increase in relative abundance of *glutinosus* in the area that apparently retains more moisture in the course of the year may be ascribed to greater sensitivity to evaporation of that species as compared with *cinereus*. The interpretation is also in accord with published evidence, which indicates that *cinereus* can withstand a greater percentage of water loss than *glutinosus*.

2. At Castle Rock as well as in the vicinity of the Biological Station *P. g. glutinosus* occurs under logs more often than *P. c. cinereus*, although both species also occur under rocks. However, when data for the two species in each area are compared statistically, the differences are not significant or barely so. Any differences that may exist can probably be ascribed to the same factors, principally moisture and the greater sensitivity of *glutinosus* to desiccation, that affect the relative abundance of the two species in the areas compared.

3. Comparisons of substratum temperatures for samples of salamanders from two areas on Salt Pond Mountain and two areas in the Balsam Mountains indicate that no significant difference exists between the mean thermal levels of two or more species inhabiting the same area. However, a species living at one mean thermal level in one area may be found in another at a significantly different level

4. Moisture requirements doubtless restrict the activities and distributions of terrestrial salamanders, but their body temperatures closely approximate those of their normal surroundings, especially the substratum. The majority of the species investigated were living under moist conditions where mean substratum temperatures varied from 15° to 18° C. Other evidence indicates that most terrestrial salamanders live in areas where the temperature of their surroundings rarely exceeds 20° C. Higher temperatures are tolerated by some aquatic species, and some salamanders can remain active at temperatures only a few degrees above freezing. But there is no evidence that salamanders exercise any control over the thermal level of their body. Were they sensitive to thermal changes they could, by means of their movements, avail themselves of differences in the temperature of the substratum that occur in time and space. Whereas lizards in their natural habitat maintain the body temperature at a mean level characteristic of each species, salamanders apparently lack this ability. It may be concluded that salamanders are not markedly sensitive to changes within the range of temperatures tolerated.

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POSTGLACIAL FORESTS IN THE GRANDE PRAIRIE–LESSER SLAVE LAKE REGION OF ALBERTA, CANADA [1]

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Ten peat sections from as many muskegs were taken along the highway between Athabaska, Alberta and the British Columbia-Alberta border, a distance of about 350 miles (Fig. 1). An eleventh section was obtained about 12 miles south of Smith. Principal towns on this highway are High Prairie, about 30 miles to the west of Lesser Slave Lake, and Grande Prairie which is about 60 miles east of the British Columbia-Alberta border, and 370 miles from Edmonton by highway. Athabaska is about 100 miles north of Edmonton (Fig. 1).

Most of the sites of accumulations are of the muskeg type which apparently developed on more or less flat terrain without an initial aquatic stage. This is evidenced by the absence of limnic peat underlying the fibrous Sphagnum peat as well as the dearth of pollen grains of hydrophytic plants in either the clay-silt or in the lowest organic sediments. In a previous paper the author distinguished between the typical bog and the muskeg, largely upon the basis of these criteria (Hansen 1949a). Although the mature stages of bog and muskeg are similar with respect to both species and many physical characteristics, the term muskeg has been applied largely to sites of organic sedimentation in the arctic and subarctic. In this region the muskegs are comparatively shallow and cover vast expanses, many square miles in some cases, and lie on flat terrain or in broad shallow basins. It is possible that the development of muskegs on flat terrain in a region of comparatively low precipitation as in Central Alaska, Yukon Territory, and the area of this study was favored by the presence of permafrost. Permafrost prevents subsurface drainage and causes the water table during the summer to rise to the surface. The abundance of moisture at or on the ground surface promoted the growth of tundra and muskeg plants, which in turn, pro-

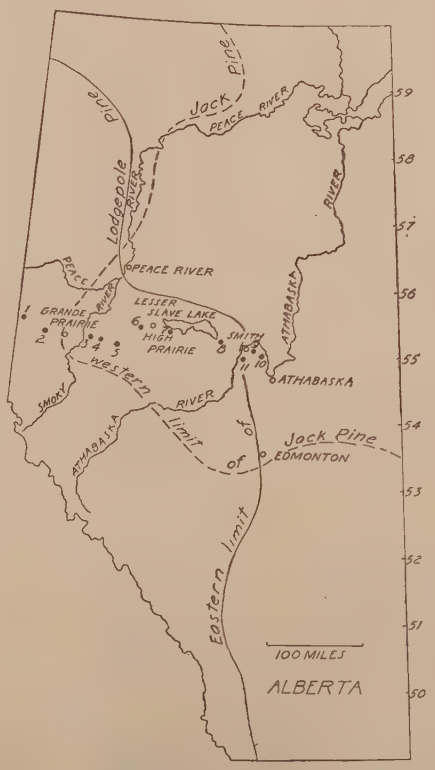

FIG. 1. A somewhat generalized map of Alberta showing location of muskegs and the range limits of lodgepole and jack pines. After Moss (1932, 1949).

[1]The author is grateful to the American Philosophical Society for a grant from the Penrose Fund to defray the expenses of the field work, to the John Simon Guggenheim Memorial Foundation for a fellowship during 1947–48 which gave him the time for the pollen analysis, and to the General Research Council of Oregon State College for a grant for certain laboratory supplies and equipment.

vided insulation for the permafrost and raised the water table. Once started, Sphagnum moss and sedges served to hold the moisture still higher and favored continued growth of muskeg plants and peat accumulation. Sampling of the muskegs of this study revealed no permafrost either in the peat or the underlying inorganic clays and silts. The author believes, however, that permafrost may have existed in this area at the time of muskeg inception, and, in fact, was responsible for the conditions necessary for their development. The occurrence of muskegs as far south as Edmonton, Alberta, suggests that permafrost may have extended as far south as this latitude, and has since retreated northward with the advent of a warmer climate, perhaps during the postglacial warm, dry maximum.

The muskeg flora has many species in common, including black spruce (*Picea mariana*), Labrador tea (*Ledum groenlandicum*), cranberry (*Vaccinium oxycoccus*), blueberry (*V. uliginosum* and *V. vitis-idaea*), bog birch (*Betula glandulosa*), bunchberry (*Cornus canadensis*), cloudberry (*Rubus chamaemorus*), crowberry (*Empetrum nigrum*), *Sphagnum* spp., and others. All muskegs except the one south of Smith support an abundant growth of black spruce, but lodgepole pine (*Pinus contorta latifolia*) was noted on only two, while larch (*Larix laricina*) was observed on five of them. Some of the muskegs are miles in extent and these two arborescent species may well be present on more of them. White birch (*Betula papyrifera* var.) occurs on several of the muskegs in burned areas. Hairy cap moss (*Polytrichum* sp.) was also observed commonly where the bog surface had been burned as was also the reindeer moss (*Cladonia rangifera*). Other species noted are *Potentilla palustris, Chamaedaphne calyculata, Andromeda polifolia, Kalmia polifolia, Drosera rotundifolia, Carex* spp., and *Salix* spp.

The muskegs are numbered from west to east, and the following list gives the location in relation to some landmark or town:

Section	Location
1.	3 miles east of the British Columbia-Alberta border.
2.	16 miles west of Grande Prairie, near Saskatchewan Lake.
3.	5 miles east of Smoky River, 25 miles east of Grande Prairie.
4.	20 miles east of Smoky River.
5.	near west end of Sturgeon Lake, about 45 miles east of Grande Prairie.
6.	6 miles west of Triangle, 15 miles west of High Prairie.
7.	30 miles east of High Prairie.
8.	6 miles east of Slave Lake village.
9.	10 miles east of Smith.
10.	20 miles east of Smith.
11.	12 miles south of Smith.

The thickness of the sections varies from 1 to 2.5 meters, with an average of about 1.95 m. This includes in some cases a half meter of clay-silt upon which the fibrous Sphagnum peat immediately lies. The almost complete absence of pollen grains in this inorganic material indicates that it constitutes the original pre-muskeg surface, which has since undergone gleization as a result of the waterlogged conditions caused by the overlying organic mantle. Volcanic ash fragments occur in most sections near the surface, while they are also present in several of the sections at a lower horizon. The glass in the upper levels may be from the eruption of Mt. Katmai on Kodiak Island which occurred in 1912, while the lower ash apparently came from an earlier eruption of unknown location. A second lower layer of ash occurs in two bogs west of Edmonton, and muskegs along the Alaska Highway in the Yukon Territory also contain volcanic glass at two different stratigraphic levels (Hansen 1949b). The source of the former has been suggested as Glacier Peak in north-central Washington, but the distance of the Yukon muskegs from this site hardly favors this source. It should be said, however, that the postglacial eruption of Glacier Peak was of considerable magnitude and its ash dispersed extensively to the east and north. A peat section at Newman Lake, 20 miles northeast of

Spokane, shows a layer of pure volcanic glass almost a foot thick (Hansen 1939). The Grande Prairie-Lesser Slave Lake region lies about 550 miles north of Glacier Peak. Pumice noted in peat sections from bogs in south-central British Columbia indicates that postglacial volcanic activity occurred in this region.

In preparation of the peat for pollen analysis the potassium hydrate method was used (Hansen 1947). From 100 to 200 pollen grains of indicator species were identified from each level except from the underlying clays and silts. In the few inorganic horizons included in the profiles, not less than 50 pollen grains of significant species were identified. It seems possible to separate white spruce (*Picea glauca*) from black spruce, and lodgepole from jack pine (*Pinus banksiana*) with some degree of accuracy by means of the size range method (Hansen 1947). This was done for some sections, but pollen profiles of the individual species are very irregular with uninterpreted fluctuations from level to level. A pine pollen, more minute than that of either lodgepole or jack pine, was noted sporadically in most of the sections, but most abundantly in the more easterly located muskegs. As most of the sites of this study lie within the area of overlapping ranges of lodgepole and jack pine, it is possible that this small pollen grain represents the hybrid between the two species which occurs in the region (Moss 1949). The occurrence of ericad pollen in the lowest levels lying directly upon the inorganic clay and silts, and the abundance of conifer pollen also, indicate the forests already existed in the area when the peat accumulation began. Other pollens in the lowest horizons include those of alder, willow, sedge, and birch.

Forests of the Region

The Grande Prairie-Lesser Slave Lake region encompasses the meeting place of three climaxes. These are the boreal forest, the subalpine or Cordilleran forest, and the grassland. The transect of muskegs from which the peat sections were obtained actually traverses the zone of overlapping ranges of species of the boreal and subalpine forests. The boreal forest extends across the continent from Labrador into Alaska. It is bordered on the north by the tundra and on the south by the lake forest and grassland, and contacts the main body of the subalpine forest near the eastern front of the Rocky Mountains in Alberta, British Columbia, and the Yukon. In Alberta, the climax or primary arborescent species of the boreal forests are white spruce and balsam fir (*Abies balsamea*). Jack pine, a subclimax species in the boreal forest, which finds its westernmost range in Alberta, thrives after burning or on sandy soil. In the latter habitat it simulates a climax species, probably because of lack of competition. It is particularly abundant on the sandy outwash in the vicinity of Smith and Athabaska, and ranges almost as far west as Grande Prairie (Fig. 1). Aspen (*Populus tremuloides*) is one of the most abundant trees in the region and it has been favored by recurring fire and clearing. It is abundant in the Grande Prairie region, and in the absence of continued cultivation rapidly takes over. Larch (*Larix laricina*) and black spruce are confined largely to muskegs, with the latter being by far the more abundant. White birch is not abundant in the region and thrives as a result of fire, either on the muskeg or upland. It was noted in abundance on several of the muskegs in burned areas. Balsam poplar (*Populus balsamifera*) is locally abundant on floodplains and was noted especially in abundance along the floodplains of the Smoky and Little Smoky Rivers, and the Athabaska River farther east.

Two arborescent subalpine or Cordilleran species occur in the region. Alpine fir (*Abies lasiocarpa*) is a climax dominant which ranges eastward to central Alberta but is not common (Halliday 1943). Although the ranges of alpine fir and balsam fir almost meet in north-central Alberta, as yet they have not been found to overlap. More abundant

is lodgepole pine which extends eastward in Alberta to Smith and almost to Edmonton. It also occurs as an outlier in the Caribou Mountains south of Great Slave Lake (Raup 1935). Lodgepole is subclimax throughout its vast range and owes its persistence to burning and clearing or edaphic disturbance. It forms vast pure stands along the Alaska Highway in British Columbia and the Yukon, but becomes less abundant eastward in the Grande Prairie-Lesser Slave Lake region. The ranges of lodgepole and jack pine overlap in this region with the greatest concentration of jack pine in the eastern part and lodgepole pine in the western portion. Lodgepole occurs on the lighter soils and on muskegs with black spruce and larch. As mentioned earlier the pine pollen of this study is obviously a mixture of the two species. Moss (1949) has noted the occurrence of hybrids between lodgepole and jack pine and has mapped their overlapping ranges. It is probable that the pollen of the hybrid also occurs in the sections, as most of them lie within the range of the hybrids. It is interesting to note that Moss observed more hybrids farther east of the range of overlap than to the west, suggesting the influence of prevailing westerly winds during anthesis. Moss (1932) extends the Cordilleran forest eastward to Athabaska, probably due to the ranges of lodgepole pine and alpine fir this far east.

South of the boreal forest and east of the subalpine forest in Alberta, in order are the Poplar area, the Parkland, and the Prairie (Moss 1932, 1944; Moss and Campbell 1947). It is possible that these vegetation provinces lay farther north during the postglacial warm dry maximum, and have since moved southward as the climate became moister and cooler. This is suggested by the fact that the southern fringe of the boreal forest occupies black soils that have become partially podsolized into transition or gray soils (Odynsky 1945). In the Grande Prairie and Peace River region there are extensive grassland areas that may have persisted from greater expanses during the xerothermic interval.

The heterogeneity of the forests in the region of this study is well suggested by the term "Mixedwood" section applied by Halliday (1937). Outliers of Halliday's Aspen Grove section which lies adjacent to the praire of southern Alberta occur in the vicinity of Grande Prairie, Peace River, and west of Lesser Slave Lake. The dark soils of this section suggest former grassland which was replaced by aspen in more recent time. The Aspen Grove section has been largely cleared and today is utilized for growing grain, chiefly wheat. The Mixedwood section is further fragmented by extensions of the Foothills section eastward from the foothills of the Rocky Mountains, forming an ecotone which in effect constitutes the merging of the boreal and subalpine forests. The muskegs of this study lie largely within this ecotone. There seems to be every conceivable combination of the species mentioned above, with patchwise mixtures of aspen, white spruce, birch, balsam poplar, the firs, and even grassland. These species also occur in pure stands. This mixture has been fostered by fire and clearing in conjunction with soil and exposure. It seems probable that over the region white spruce would become the predominant tree and occur largely in pure stands if there were no disturbance for a few hundred years. In the sandy areas jack pine would probably persist even in the absence of fire, while on the south slopes aspen would also thrive without the benefit of continued disturbance. The three climax types or geographic elements, the boreal and subalpine forests and grassland, were probably separated by the Late Wisconsin glacier, and have since migrated into the region from their proglacial refugia. The dynamics of adjustment are still progressing and with the constant changes in environment caused by fire and clearing no ultimate phytogeographic pattern can be foreseen. With hybridization occurring, natural selection of biotypes tak-

ing place, and continuing migration of some of the species, new combinations of the floristic elements may gradually develop.

Glacial relationships in the Grande Prairie-Lesser Slave Lake region are unknown and uncertain. It seems improbable that the Late Wisconsin Cordilleran ice was sufficiently nourished on the east flanks of the Rocky Mountains at this latitude to extend this far east (Flint 1947). It is also problematical whether the Keewatin ice sheet, moving south and west from centers in the Hudson Bay region, reached the area of this study during the last glacial stage. Cameron (1922) has shown that glacial lobes extended south and west up the Peace and Athabaska river valleys in his study of postglacial lakes in the MacKenzie River basin. He does not show them reaching as far south as the region of this study, although it is doubtful if he considered these lobes as the maximum extension of the Late Wisconsin ice. Bretz (1943) located the Altamont (Late Wisconsin) moraine about 75 miles east of Edmonton, and traced its eastern border northwestward in Alberta north to latitude 54°. Extension of the Altamont moraine border in the same general direction to meet with the Athabaska and Peace river lobes would indicate that the Grande Prairie-Lesser Slave Lake region was not covered by Late Wisconsin ice, and that there was an ice-free corridor a hundred or more miles in width in western Alberta and northeastern British Columbia. The level terrain, extensive lacustrine deposits, and the persistence of broad shallow lakes in the Grande Prairie region today denote the existence of vast proglacial lakes ponded against the glacier to the northeast during the maximum extension of the Late Wisconsin glacier.

Postglacial Forest Succession

Interpretation of the pollen profiles into terms of forest succession and paleic composition is qualified by the same conditions as those along the Alaska Highway in British Columbia as well as those in other regions (Hansen 1950). Perhaps the most significant is the almost complete absence of *Populus* pollen which is not well preserved in peat. While aspen and balsam poplar are the only species of this genus in the region, the former undoubtedly has been an important and abundant component of the prehistoric forests. The influence of fire as reflected by the successional relationships of aspen to pine, spruce, and grassland would undoubtedly be manifested many times in the sedimentary columns if aspen pollen were representatively preserved. Although birch pollen is fairly abundant, no attempt has been made to separate bog birch from white birch. Both are present on the muskegs but the latter is also present on the uplands. In view of its present sparseness in the forest complex, however, it may be that white birch was never abundant in the past. Its fluctuations, like those of aspen, would probably express a pyric influence. The occurrence of black spruce on muskegs and white spruce on adjacent uplands denotes their differences in environmental requirements. Consideration of all spruce pollen in a single profile may present a false picture of forest succession inasmuch as only white spruce pollen is an indicator of adjacent upland forest succession. Individual profiles of the two spruces based upon their pollen separation by the size range method, however, presents noncoordinated and uninterpreted profiles (Hansen 1950). A consolidated profile produces less erratic fluctuation and the indicated successional trends seem to be more logical. Peculiar to this study is the fact that both lodgepole and jack pine, and possibly their hybrid, are represented by their pollen, at least in the more eastern sections. A study of the pollen size ranges of the two pines denotes that lodgepole pollen runs slightly larger than that of jack pine. Individual profiles of these two species would add little or no value to this study as far as succession is concerned, although accurate separation of

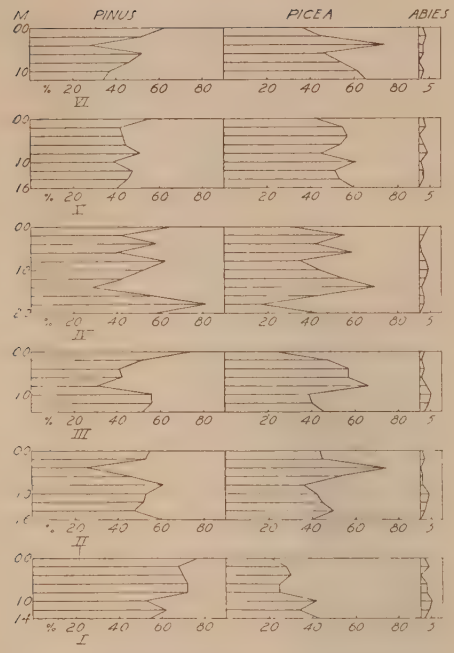

FIG. 2. Pollen diagrams of six muskegs beginning at the west end of the transect.

their pollen would perhaps reveal their postglacial migrations in this region. Perhaps of greater significance is the fact that the pines produce more pollen than the other species and at a much earlier age. It can be assumed with little doubt that the pines are somewhat overrepresented in this study. Although fir is scarce in the region, the occurrence of both alpine and balsam fir pollen indicates the muskegs are within range of pollen dispersal of one or both of these species. Fir pollen in the more westerly muskegs has been identified as that of alpine fir, while pollen of both species was noted in the more eastern bogs. This suggests that the prevailing westerly winds during anthesis carried alpine fir pollen eastward, while preventing balsam fir pollen from drifting westward.

The paucity of pollen from other species causes the profiles of spruce and pine to fluctuate conversely to each other throughout the region. Their total proportions at each level equal almost one hundred per cent because that of fir is negligible. While the picture of their relative abundance in adjacent areas denoted at any one horizon is probably accurate wthin the limits of pollen analysis, their fluctuations from level to level may be often merely relative. A decimation of one species may be reflected by the recorded increase of the other although there was no actual increase in the abundance of the latter. This is also true when several species are involved, but it is accentuated with fewer species represented. It is true that pine produces more pollen than spruce, but this is at least partially offset by the prevalence of black spruce on the muskeg.

In general, pine has been progressively less abundant eastward during the time represented by the sedimentary columns. The major deviation from this recorded pattern is in section 11, south of Smith (Fig. 3). This muskeg lies on sandy outwash and jack pine has been predominant in the absence of spruce competition. With the exception of this section, the average of pine proportions is highest in the westernmost muskeg, which shows 66 per cent. It then declines eastward to as low as 36 per cent in section 8 about six miles east of Slave Lake (Figs. 2, 3). The average of pine and spruce proportions for each profile is shown in Table I. Although the pollen records of lodgepole and jack pine are not treated separately, pollen size frequencies indicate that lodgepole pollen is far more abundant than that of

TABLE I. *Pine and spruce pollen averages for each section*

Section	1	2	3	4	5	6	7	8	9	10	11
Pine	66.1	47.1	50.5	53.2	45.2	44.0	36.3	36.0	42.2	38.7	69.4
Spruce	31.0	48.8	47.0	44.7	53.0	54.3	63.0	62.3	57.0	61.0	26.6

jack pine in all sections except 9, 10, and 11. It seems probable and reasonable that lodgepole survived in ice-free areas in western Alberta and possibly in more localized areas in northeastern British Columbia during the Late Wisconsin glaciation and then migrated eastward as the Keewatin ice retreated. Jack pine must have moved into this region from the south and east from its proglacial persistence south of the ice in the Lake states. Both species may be extending their ranges at present and their overlapping ranges today probably have developed in comparatively recent time, perhaps within the past few centuries. In only one section is either spruce or pine predominant throughout, and that is pine in the westernmost muskeg (Fig. 2). Extensive stands of lodgepole south and west of Grande Prairie may be responsible for this, as well as its occurrence on the muskeg.

Although only pine and spruce are represented by the bulk of the pollen, there seem to be several consistent trends and patterns, both regional and chronological. Spruce is predominant in the lowest pollen-bearing level in seven sections (Figs. 2, 3). This is consistent with its recorded trend along the Alaska Highway in British Columbia, where it is represented as predominant in 14 of 17 sections for a distance of over 500 miles (Hansen 1950). Pine preponderates spruce at the bottom in the four westernmost sections where it is recorded to over 50 per cent in each. In none, however, does pine supersede spruce by more than 20 per cent. Farther south in Alberta in the vicinity of Edmonton near the southern border of the boreal forest, however, pine is predominant in 6 of 7 sections at the bottom, while west of Edmonton, 3 or 4 sections reveal pine as most abundant (Hansen 1949a, 1949b). The minimum and maximum proportions of pine at the bottom are 26 and 60 per cent respectively with an average of 44 per cent. For spruce the minimum and maximum are 40 and 70 per cent respectively, with an average of 56 per cent. Considering the more prolific pollen production of pine, it seems probable that over the region as a whole, spruce was somewhat more abundant than pine when the lowest pollen-bearing sediments were deposited. In all but two sections pine declines to its minimum between and top, which occurs at various stratigraphic positions in the profiles. The lowest proportion for pine is 22 per cent in section 7 (Fig. 3).

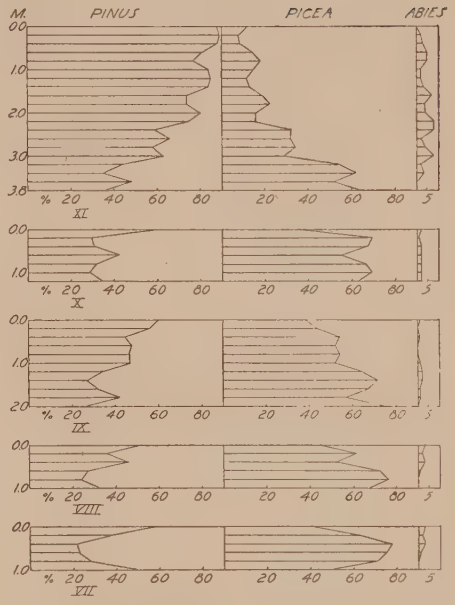

FIG. 3. Pollen diagrams of five muskegs. No. 11 is located 12 miles south of Smith on sandy outwash.

Most profiles show pine as initially increasing upward from the bottom, then diminishing, again increasing, then declining, and finally expanding in the upper levels to attain its maximum in all but one section. In all sections pine reaches higher proportions at the top than does spruce. The minimum and maximum proportions of pine at the surface are 50 and 88 per cent respectively with an average of about 65 per cent. Spruce shows a minimum and maximum at the top of 12 and 47 per cent respectively with an average of about 34 per cent. Al-

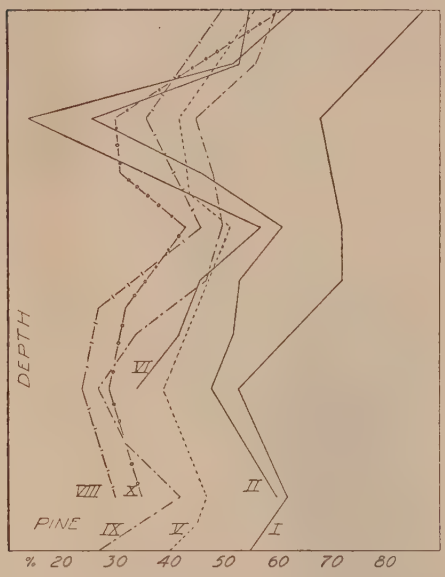

FIG. 4. Pollen profiles of pine from seven muskegs, showing possible correlation of the major trends.

though in some cases the difference between pine and spruce at the top is non-significant, it is probable that pine has been generally more abundant than spruce during the last century or so.

Conversely to pine, spruce attains its maximum between the bottom and top in most sections, indicating that conditions became more favorable for its expansion as postglacial time passed. The early postglacial preponderance of spruce in this region suggests the influence of a moist and cool climate in the wake of the retreating glacier. Expansion in some areas and maintenance of this initial abundance in others indicate continued favorable conditions for spruce which may have been sufficient moisture and absence of fire for a long time. Sharp and broad fluctuations in some of the profiles may express the occurrence of fire in local areas that favored pine, followed by fire-free periods which permitted spruce resurgence. That some regional influence was at play, however, is suggested by the similarity of pattern in these fluctuations in several of the profiles (Fig. 4). In spite of the alternating fluctuations, the over-all trend of pine expansion in the upper levels suggests an ever increasing pyric influence probably augmented by a drying climate. The general postglacial expansion of lodgepole pine also along the Alaska Highway in British Columbia and westcentral Alberta denotes that this entire vast region was subjected to environmental adjustments that were more favorable for pine than for spruce.

Fir (*Abies*) pollen is too scanty to be of any interpretative significance, except that it has never been abundant in the region. In the three westernmost sections fir is best represented near the bottom, but in the other sections it portrays no particular trend. Two sections reveal the fir maximum in the upper half, while section 11 shows the highest proportions of fir throughout, but with no fluctuations relative to those of spruce or pine (Fig. 2, 3).

Other species of tree pollens noted are *Betula, Alnus,* and *Populus.* Of these, birch is the most abundant and consists of both bog and white birch pollens. Aspen pollen is too scarce and sporadic to be of any significance, although 10 aspen pollen grains were counted in the uppermost level of section 11. Grass representation is also scanty, and its pollen most abundantly noted in the same section. This may be accounted for by the fact that the muskeg supports a luxuriant growth of *Muhlenbergia glomerata* var. *cinnoides.*[2] The small quantities of grass pollen noted in the other sections occur in the upper horizons, denoting perhaps the effects of clearing, cultivation, and fire in more recent times. There is no evidence of a grass expansion during the postglacial warm, dry maximum such as is suggested in the pollen profiles from muskegs in the vicinity of Edmonton. Here a pronounced influx of grasses, chenopods, and composites in the middle third of most sections has been interpreted

[2] Identified by E. H. Moss, University of Alberta.

as an expression of the xerothermic interval (Hansen 1949a, 1949b). The occurrence of Douglas fir (*Pseudotsuga taxifolia*) pollen grains in the upper levels of section 11 denotes that pollen of this species can be airborne great distances, as the nearest known Douglas fir is near Jasper, more than 200 miles to the southwest.

The chronology of the recorded forest history of this study is indefinite. Although it is not certain that the region was entirely covered by the Late Wisconsin ice, the occurrence of many large lakes in the region ponded against the northeastward retreating Keewatin ice may have prevented migration of forests into the region until the lakes were drained or the ice had receded or both. As mentioned above, the region is the meeting place of the boreal and subalpine (Cordilleran) forests with the grasslands not far to the south. It seems probable that jack pine and balsam fir migrated into the region from the south and east. The writer believes that the Cordilleran species, lodgepole pine and alpine fir, migrated from the west where they persisted in an ice-free corridor in western Alberta and smaller refugia in the northern Cordillera, northeastern British Columbia, and in west central Yukon during the Late Wisconsin glaciation (Hansen 1949a, 1949b, 1950). The occurrence of lodgepole pine on the apparently unglaciated higher portions of the Caribou Mountains in northern Alberta may represent another refugium (Raup 1946). The increase of high proportions of lodgepole pollen in the lower levels of muskegs in this study, in west central Alberta, and along the Alaska Highway in British Columbia, denotes the existence of a nearby source for early postglacial migration of this species. If it did not persist in the refugia mentioned above it would seem hardly possible that it would be so abundantly represented at the bottom of muskegs at this latitude and farther north.[3] If the entire region of Alberta and British Columbia were covered by ice simultaneously, it would be more logical to find spruce and fir represented by practically 100 per cent at the bottom of the muskegs. The present range of spruce far north of pine indicates that it would have been better able to persist closer to the glacier and thus migrate into deglaciated areas sooner than lodgepole. This interpretation is supported by Hultén's theory with respect to the survival of boreal flora in unglaciated areas in the Upper Yukon River Valley and parts of Alaska (Hultén 1937). Aside from the firs and pines, western and eastern varieties of white spruce, larch, and white birch occur in northern Alberta (Raup 1946). While it is uncertain as to when these species became variegated, it is conceivable that the western varieties *Picea glauca albertiana, Larix laricina alaskensis,* and *Betula papyrifera neoalaskana* postglacially invaded the area from refugia to the northwest while the typical species advanced from the southeast. Black spruce and aspen may have reached the Grande Prairie-Lesser Slave Lake region from either or both the southeast and the west.

[3] Unpublished data from Yukon muskegs, being studied by the author.

Summary

Pollen profiles from eleven peat sections in the Grande Prairie-Lesser Slave Lake region of Alberta reveal that pine (*Pinus*) is more abundantly represented in the western part and becomes less abundant eastward with the exception of the easternmost section which lies on the pine-forested sandy glacial outwash north of Edmonton. The pollen proportion averages of pine decrease eastward while those of spruce (*Picea*) conversely increase. In nine sections pine is recorded to its maximum at the top while spruce attains its maximum at some point between the top and bottom. The expansion of pine in the upper levels may reflect the influence of fire and a drier climate in more recent time. Fir (*Abies*) is only slightly represented and its trends do not seem to be significant. The absence of

aspen (*Populus*) pollen, due to its poor preservation, undoubtedly distorts the pollen profiles and presents an incomplete picture of forest succession.

The chronology of the recorded forest history is not clear because it is not known whether the region was covered by the Late Wisconsin ice, although vast lakes in the region probably prevented extensive forest development until postglacial time. The relative shallowness of the muskegs does not point to great antiquity, and they may have developed since the warm, dry maximum. The region was postglacially invaded by species of the subalpine Cordilleran forest, the boreal forest and the grassland. Species of the Cordilleran and boreal forests may have persisted in refugia in northeastern British Columbia and central Yukon during the last glaciation.

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EFFECTS OF THE REMOVAL OF THE FISH POPULATION ON THE FISH-FOOD ORGANISMS OF A LAKE

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Almost all of the macroscopic aquatic organisms can serve as food for fishes under certain conditions and the many quantitative and qualitative studies of the standing crops of fish-food animals have been of value in estimating the capacity of a body of water to produce fish. While investigations of the production of fish-food animals are numerous, the majority of these studies are based upon summer season collections only. A very few of the workers have made estimates of production of invertebrates (Lundbeck 1926; Miller 1941). Ricker (1946) presented an analysis and review of the literature with a discussion of certain problems of the dynamics of production and also delineated the fundamental concepts of productivity which have an ecological application. Clarke (1946) has outlined concepts of productivity in a marine area. Certain of the interrelationships of a fish population and the invertebrate fauna in one of Michigan's lakes have been considered by Ball (1948). The present report is concerned with a study, in this same lake, first, of the composition of the invertebrate fish-food population for a period of three years and, second, of the responses of these organisms to the removal of the fish population.

Description of the Lake

Third Sister Lake, Washtenaw County, in southeastern Michigan, with an area of 10 acres has a private status since it lies within a forested tract owned by the University of Michigan. The lake is approximately 60 feet deep, and stratifies chemically and thermally in the summer. There is no permanent inlet or outlet, the water coming from surface runoff from the surrounding hills, and draining, on rare occasions, through an outlet leading into a swamp. The lake has a steep drop-off into deep water and a narrow shoal area around much of its perimeter.

Collection of Bottom Fauna

Benthic organisms were collected at intervals from May 1939 through June 1942. Collections were made in two ways during the first year of the investigation. Large collections of the higher aquatic plants were made, weighed, and the organisms removed, identified, and tabulated. In addition to these, collections in the littoral zone were made with both the Ekman and the Petersen dredge. In subsequent years the samples were taken only by the dredge to make the data from the collections more uniform and facilitate comparisons with the results of other workers. Weekly collections were made from a boat during the open water period, which on this lake extended from about the last week in March to mid-December, and through the ice cover the remainder of the year. All organisms were removed while still alive, identified as far as possible within the limitations of the problem, and evaluated both numerically and volumetrically.

All sampling was carried out in the littoral zone of the lake since one of the aims of the investigation was to determine the relationship between the food available to the fish and the food actually taken by the fish. It has already been reported (Ball 1948) that these fish were found to be feeding very little during the months when the lake was covered with ice and that at other periods almost all of their food came from the littoral zone.

Fish Population Analysis

As part of the overall investigation of the aquatic resources of the lake the fish

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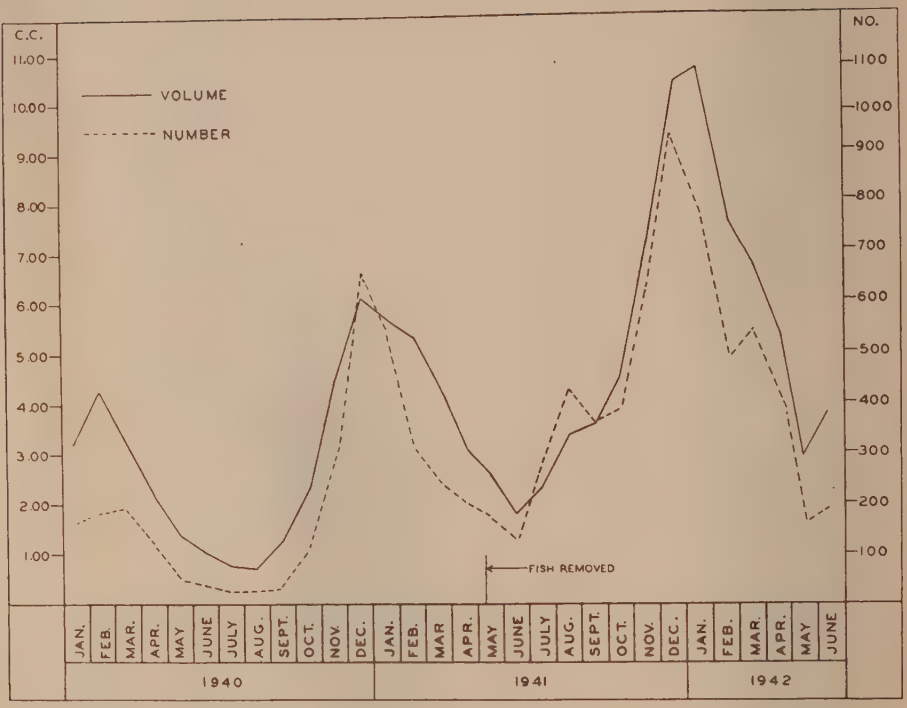

FIG. 1. Seasonal fluctuation in volume and number per square foot of benthic invertebrate fish-food organisms.

population was removed by poisoning on May 6, 1941 and an effort made to recover all fish (Brown and Ball 1942a). The fish population, as determined by those recovered following poisoning, consisted of 866 pounds of which 537 pounds were bluegills. It was estimated that 85 per cent of the fish (731 pounds) in the lake were directly dependent upon the invertebrate population that was being sampled. It is possible, in the light of later investigations of recoveries of fish following poisoning (Ball 1945; Krumholz 1950) that the fish population was larger than the above estimate would indicate.

The magnitude of a standing crop cannot be interpreted directly as a measure of the rate of production but in lieu of accurate information concerning such production the standing crop of fish food has been widely used as a relative measure of food productivity. Alm (1922) working on Swedish lakes found a relationship between the annual yield of fish and the summer standing crop of benthic organisms. This he described as the F/B coefficient.

From Third Sister Lake we have data on the standing crop of benthic organisms and also upon the crop of fishes which fed upon it. In this study no effort was made to establish production on an annual basis, but only to record annual fluctuations in the standing crop of invertebrates important as fish food and the response of these organisms to the removal of the fish population dependent upon them.

SEASONAL FLUCTUATION OF THE INVERTEBRATE POPULATION

The data for the collections of fish-food organisms for the period from May, 1939 to June, 1942 are shown in Appendix. In Appendix, the first year's collections represent only the dredge-collected samples, although the plant collections showed

essentially the same seasonal changes with a low point in volume and numbers in June and a maximum in early winter.

The same definite pattern of seasonal abundance and scarcity of benthic organisms with the low point in early summer and the peak in early winter is shown by the collections following the first year (Fig. 1). The greatest reduction of organisms occurred following the spring break-up of the ice and subsequent warming of the water. The emergence of many of the insects having a terrestrial phase in their life cycle occurs at this time.

Following this emergence there was an interval during the spring months when the fish-food organisms were very scarce in the lake. This is the time immediately following the ovipositing of the insects and many of the organisms are present in the egg stage or as early instar larvae. Apparently many of these were lost in the washing of a sample or were not recovered in sorting a sample.

With the hatching of the eggs and growth of the individual organisms the number and volume of bottom fauna increased rapidly throughout the summer until a peak was again reached about the time of the formation of the ice cover. The annual maximum was reached at about the time the ice cover forms, following which there was a decline in number and volume of organisms which continued until the break-up in the spring. The reduction of organisms during this winter period was considerable and must be attributed to causes other than emergence since emergence is impossible during this time.

The reasons for the reduction of organisms during the closed-in period are not well understood. It may be presumed that there is a constant mortality among the invertebrate population as a result of predation by other members of the community and as a result of other causes. This mortality occurring at a time when there is little replacement, would be reflected in lower numbers in the samples.

A similar trend in the seasonal distribution of profundal organisms from Third Sister Lake has been shown by Eggleton (1931). His data show a striking similarity in seasonal abundance and paucity of organisms when compared to data relating to forms within the littoral zone. Great though these similarities may be there is no obvious connection or common cause, since Eggleton was working, first, with organisms occurring within the 18 meter contour where oxygen-free conditions occur during a considerable part of the late winter and, second, with species entirely foreign to the littoral zone.

Lindeman (1942) also observed increasing numbers and volumes of bottom organisms until the ice cover formed, followed by a gradual decline through the early part of the winter with a greater loss, later in the winter, associated with anaerobiosis. In Third Sister Lake, however, there was no time when lack of oxygen could have been a factor in the similar decline of organisms. Chemical analyses were taken each week for the entire three year period and at no time was there any evidence of low oxygen or of other conditions which might have adversely affected the invertebrates of the littoral zone.

The reduction in the volume of organisms occurring between the maximum, which usually occurred in December, and the first possible emergence period amounted to approximately 50 per cent of the maximum total volume. It seems unlikely that this reduction can be accounted for on the basis of predation by the forage fish (chiefly bluegills) in the lake since not only did the same decline occur during the winter of 1941–42 when no fish were present, but winter food studies (Ball 1948) of the fish of this lake have shown that very little food was taken by the bluegills during the period of ice cover. It appears that fish of certain lakes do not feed actively in winter and that Third Sister Lake is in this class of lakes. By the time of ice formation on the lake the fish had a heavy accumulation of fat, which persisted until the time of the break-up of the ice cover in the spring.

It is suggested that there may be a correlation between the winter feeding habits of fish and the amount of fat accumulation.

Effect of the Removal of the Fish Population

On May 6, 1941 the lake was treated with rotenone (Brown and Ball 1942a) and all fish possible recovered. That the poisoning did not appreciably reduce the littoral zone invertebrate fauna has been well established (Brown and Ball 1942b), although the poison did kill almost all of the *Chaoborus* larvae. The poison also killed many of the leeches and aeschnine dragonflies but the number or volume of these was only a minor fraction of the total number or volume of organisms present in the lake.

The poisoning took place at about the time when the organisms should be expected to be at the annual minimum in the lake, and as may be seen in Figure 1, the number and volume did not reach so low a point as during the preceding year, and the upturn in volume of organisms per unit area of bottom was much sharper than during the preceding year. The volume of organisms increased rapidly until it reached a peak in December at a level nearly twice that of any other period during the three collecting years. Following this peak in December the organisms were reduced greatly during the period of ice cover and still more during the emergence period following the break-up of the ice.

While sampling was not carried out long enough in the summer of 1942 to be certain, the data suggest that the volume of organisms reached the annual minimum in May and was beginning to increase in June. If this was true, then the minimum volume for the post-poisoning period was reached at a level nearly three times that of the two years when fish were in the lake.

The fiducial limits of estimates based upon sampling and the adequacy of sampling in the profundal zone have been discussed by Deevey (1941). In comparison, the nature of sampling in the littoral zone seems to be different for there is a great variety of organisms each having its own ecological niche and successive

Table I. *Average volume of organisms per square foot of bottom, by month, for comparison of differences among years and months, with an analysis of variance of the logarithms*

Month	Year			Mean
	1939–40	1940–41	1941–42	
May	1.57	1.30	2.33	1.73
June	.58	.93	1.46	.99
July	.59	.83	3.10	1.51
August	1.41	.88	3.54	1.94
September	1.38	1.45	3.45	2.09
October	1.52	3.00	5.65	3.39
November	3.06	5.85	8.64	5.85
December	1.79	6.26	12.25	6.77
January	2.06	5.21	9.12	5.46
February	4.22	5.26	5.98	5.15
April	1.33	2.90	7.55	3.93
Mean	1.77	3.08	5.73	

Source of variability	Degrees of freedom	Sum of squares	Mean square	"F" ratio
Total	32	4.126		
Between years	2	1.404	.702	33.1**
Year 3 vs. years 1 and 2	1	1.214	1.214	57.3**
Between years 1 and 2	1	.190	.190	9.0**
Between months	10	2.298	.230	10.8**
Error	20	.424	.0212	

samples may be quite dissimilar both quantitatively and qualitatively. The results of present techniques of sampling the littoral zone seem quite variable and it is commonly accepted that there have been no entirely satisfactory estimates of the productivity of this region.

A statistical examination of the data by an analysis of variance has been made, to determine whether the observed increase in volume of organisms following poisoning might possibly have arisen from chance variation among monthly averages based upon dredge samples. The set of 33 items used in the analysis (Table I) is made up of the average value for volume of organisms per square foot for each month listed in Appendix, with the exception of March of 1940 and 1941, and May and June of 1942. Each monthly average has been treated as a single determination, regardless of the number of dredge samples contributing to it. This set of 33 monthly values covers exactly three years, two years before poisoning and one year afterward, excluding March.

Preliminary examination of the data in Table I showed a tendency for the mean to be correlated with the variance, a condition contrary to the basic assumptions of the analysis of variance (Bartlett 1947). The logarithms of the monthly average values were examined and found not to exhibit any apparent correlation between mean and variance, and therefore the analysis was carried out with these logarithmic values.

The analysis of variance (Table I) shows that highly significant differences, in the statistical sense, exist among the three yearly values. The variability among the years may be divided into two comparisons, the first contrasting the year after poisoning with the two years before, and the second comparing the first year before poisoning with the second. While the difference between the first two years is highly significant, still by far the greater amount of the variability among years is associated with the comparison of values before and after poisoning, supporting the conclusion that the increased population of invertebrates was associated with the removal of the fish.

The average level of the invertebrate population, for the year following poisoning, based upon the logarithmic values used in the analysis of variance, was 2.6 times the average of the previous two years.

The highly significant differences among monthly values are clearly an aspect of the marked seasonal fluctuation in population density shown in Figure 1.

The standard deviation of a single monthly value, allowing for differences between years and between months, may be estimated as 0.146 (in logarithms). Following the reasoning of Winsor and Clarke (1940) this is equivalent to 40 per cent of the monthly value. This rather high standard deviation not only reflects the recognized high variability of results based upon bottom samples but also includes the effect of any differences in seasonal trends between years (the "interaction," in a statistical sense, between months and years). In comparison, the standard deviation of a single monthly value, making no allowance for differences among years or months, is equivalent to 129 per cent of the monthly value. It may be recalled that these monthly values were based upon between 5 and 144 dredge samples (Appendix).

It appears that, following the removal of the trophic levels constituting the primary and secondary carnivores, the standing crop of benthic organisms increased until a dynamic equilibrium was reached whose limits were determined by factors other than the predation by fish. This higher level of equilibrium was approximately twice the mean annual standing crop prior to the removal of the fish.

Summary

Littoral zone sampling of the fish-food organisms of a 10-acre Michigan lake has shown considerable seasonal differences in the volume and number and species composition of invertebrate organisms.

APPENDIX. *Invertebrate fauna collected by dredge sampling, 1939–1942*

Collection dates		1939								1940											
		May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Number of samples		5	5	10	17	9	19	13	12	15	16	14	24	32	15	108	144	30	25	9	5
Total area of samples (sq. ft.)		5.9	7.4	13.1	29.5	17.4	15.7	6.25	5.75	7.5	8.0	7.0	7.5	8.0	7.8	30.5	36.0	7.5	6.3	4.5	2.3
Total number of organisms		816	283	754	2,130	677	835	780	478	1,240	1,581	1,255	343	491	257	806	1,064	310	1,104	2,032	1,931
Number of organisms per sq. ft.		138	38	57	72	39	52	125	83	165	198	179	46	61	33	26	30	41	176	452	858
Total volume of organisms (cc.)		9.26	4.30	7.80	41.57	24.05	24.23	19.14	10.32	15.47	33.73	19.70	9.96	10.45	7.23	24.88	31.66	10.87	18.73	26.32	14.08
Volume of organisms per sq. ft.		1.57	.58	.59	1.41	1.38	1.52	3.06	1.79	2.06	4.22	2.81	1.33	1.30	.93	.83	.88	1.45	3.00	5.85	6.26
Anisoptera	A*	17	11	30	164	71	67	49	40	76	136	46	48	55	33	149	197	50	72	64	50
	B	1.06	1.60	2.27	12.99	8.62	6.95	6.07	3.82	7.11	15.48	6.49	3.71	3.52	2.56	16.30	22.46	3.16	5.39	4.93	5.06
Zygoptera	A	95	5	6	285	164	96	39	53	59	145	68	32	23	9	1	13	18	130	93	36
	B	1.18	.10	.10	1.35	2.09	1.00	.24	.58	.65	1.50	.91	.33	.36	.13	.01	.18	.13	1.04	.75	.38
Trichoptera	A	133	66	232	1093	292	251	180	86	82	214	84	36	27	3	45	254	104	132	370	44
	B	4.30	1.70	2.29	22.22	9.20	11.52	9.28	3.52	2.96	7.85	3.64	1.99	1.37	0.5	.84	3.89	2.51	5.34	15.07	1.84
Chironomidae	A	398	58	358	296	47	167	198	91	667	436	786	147	119	160	401	119	9	291	674	875
	B	1.25	.18	1.33	.81	.20	.82	.34	.46	1.94	2.37	4.79	.63	.50	.49	1.53	.43	0.10	1.22	2.83	4.57
Other diptera	A	0	1	20	29	0	2	2	2	2	6	0	4	3	8	3	5	3	6	3	0
	B	0	0	.70	1.21	0	.15	.35	.05	.10	.31	0	.97	1.05	3.02	1.80	1.05	.99	.58	.06	0
Ephemerida	A	7	0	26	11	1	82	63	32	54	142	32	22	26	9	1	3	0	33	42	659
	B	.10	0	.16	.05	0	.43	.11	.11	.17	.42	.10	.03	.13	.10	0	0	0	.10	.16	.90
Amphipoda	A	20	3	16	51	0	106	182	106	59	328	128	32	27	22	174	426	98	231	480	131
	B	.10	0	.10	.15	0	.45	.37	.23	.79	1.05	.40	.04	.16	.03	.22	.36	.09	.06	.24	.18
Annelida	A	8	7	13	32	10	12	3	5	6	9	9	2	1	2	18	29	7	8	9	7
	B	.20	.42	.67	.87	.95	1.49	.62	.43	0	3.26	1.42	.70	0	.10	2.99	2.15	2.07	.72	0	.81
Mollusca	A	128	80	36	165	76	54	39	42	193	108	96	19	210	6	12	18	21	198	99	25
	B	1.12	.37	.32	2.05	2.17	1.10	1.57	1.08	1.75	.85	1.85	1.36	3.35	.73	.93	1.15	.92	4.19	2.19	.33
Miscellaneous	A	10	52	17	4	16	2	25	21	25	57	6	1	0	5	2	0	0	2	0	104
	B	0	0	0	0	.82	.32	.27	.05	.05	.54	.10	.20	0	.05	.22	0	0	.10	0	.05

Collection dates		1941												1942				
		Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Apr.	May	June
Number of samples		18	32	36	46	37	6	22	14	31	20	18	8	11	10	20	16	20
Total area of samples (sq. ft.)		4.5	8.0	9.0	11.5	8.5	1.5	5.5	3.75	7.75	5.0	4.5	2.0	2.75	2.50	5.00	4.00	5.00
Total number of organisms		1,021	3,099	1,755	2,542	1,297	160	2,690	1,414	2,794	2,151	3,743	2,044	1,412	1,187	3,141	608	939
Number of organisms per sq. ft.		227	387	195	212	153	107	489	377	361	430	832	1,022	513	475	628	152	188
Total volume of organisms (cc.)		23.45	42.05	28.81	33.41	19.79	2.19	17.05	13.29	26.76	28.26	38.90	24.49	25.08	14.96	37.76	11.29	18.34
Volume of organisms per sq. ft.		5.21	5.26	3.20	2.90	2.33	1.46	3.10	3.54	3.45	5.65	8.64	12.25	9.12	5.98	7.55	2.82	3.67
Anisoptera	A*	87	109	78	125	79	6	170	77	93	72	52	26	36	39	60	19	47
	B	8.92	14.41	9.01	8.82	5.24	.82	7.58	6.40	8.76	10.85	6.55	5.90	8.55	4.04	5.39	3.45	5.29
Zygoptera	A	51	46	45	68	39	15	205	145	155	168	148	51	58	57	19	6	10
	B	.71	.43	.58	.62	.82	.10	1.52	.93	1.07	2.11	2.29	.98	1.13	.73	.40	.10	.36
Trichoptera	A	112	131	97	168	61	1	33	7	11	9	17	16	2	1	8	2	8
	B	4.51	6.65	4.21	5.87	2.78	0	.15	.14	.37	.08	1.37	4.78	.05	0	1.06	0	.13
Chironomidae	A	480	2,111	1,150	1,550	640	79	633	471	956	657	2,012	493	466	434	769	94	63
	B	2.64	11.22	7.59	9.05	2.45	.34	2.11	1.22	3.16	2.19	8.93	1.95	1.47	1.03	3.62	.38	.64
Other diptera	A	4	3	3	21	5	3	5	3	9	13	0	2	0	1	9	8	6
	B	1.28	.35	1.03	.13	1.04	.59	.37	.10	.93	.70	0	.39	0	0	.10	.05	1.06
Ephemerida	A	34	123	77	170	223	12	16	50	41	154	180	32	40	14	13	3	6
	B	.10	.42	.44	.54	.69	.10	.10	.20	.23	.46	1.01	.19	.24	.11	.07	.07	.02
Amphipoda	A	147	462	187	250	236	35	1,248	345	524	519	738	777	219	156	723	56	231
	B	.91	2.09	.70	.58	.73	.10	1.43	.49	3.06	1.84	4.43	3.26	.52	.40	2.19	.14	.96
Annelida	A	11	8	12	7	18	0	8	1	1	3	0	0	0	0	5	3	4
	B	1.32	1.39	.57	.86	2.23	0	.11	.60	.43	.90	0	0	0	0	.20	.10	.10
Mollusca	A	61	77	48	202	91	4	231	290	956	522	560	639	587	484	1,527	418	549
	B	2.83	4.89	4.52	6.94	3.81	.15	2.83	3.30	7.98	8.08	12.32	6.78	13.15	8.61	24.44	7.04	9.64
Miscellaneous	A	34	29	58	20	0	5	141	25	48	34	183	8	4	0	13	0	15
	B	.23	.20	.16	0	0	0	.85	.05	.77	1.04	2.00	.26	0	0	.29	0	.14

A—number. B—volume.

The annual maximum concentration of these organisms was reached in early winter, coinciding closely with the formation of the ice cover. Following the closing-in of the lake the invertebrate population declined steadily until the break-up of the ice in the spring, immediately following which there was a still further reduction by emergence of the adult forms of the aquatic insects. The low point of the volume and number of littoral zone invertebrates was reached by the time stratification of the lake had taken place, followed by a sharp increase until the next annual peak was reached in late fall or early winter.

The effect of the removal of the fish population upon their food supply was evaluated statistically and the results indicate clearly the level of effectiveness of the fish in reducing, or holding at a lower level, those organisms upon which the fish feed. The annual cycle of abundance and paucity of organisms following poisoning was similar to the pre-poisoning period but differed in that the volume and number of organisms did not reach as low a level during the summer period and were considerably greater at their maximum period.

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STUDIES IN HALOPHYTES. I. THE GERMINATION OF THE SEED AND ESTABLISHMENT OF THE SEEDLINGS OF FIVE SPECIES OF *ATRIPLEX* IN AUSTRALIA

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Introduction

The genus *Atriplex* (saltbush) is represented in Australia by some 30 species, most of which occur in the drier parts of the continent. All of the species are halophytic and most are palatable to stock. Of considerable importance in the inland of Australia are the five species discussed in this paper. The two robust perennials, *A. nummularia* and *A. vesicaria,* are of the greatest value as fodder, and at one time these two species occurred as the dominants over large areas. However, soon after the discovery of the western plains, the flat saltbush country was exploited, stock being introduced in such large numbers that most of the perennial bush was removed. Disappearance of the bush was followed either by invasion by less palatable plants and weeds, or by soil erosion (Beadle 1948). Consequently regeneration of the bush (or the introduction of a substitute) is today one of the major problems of the inland, and although many attempts have already been made to establish perennial bush by sowing, most of these projects have been unsuccessful; failure has resulted largely because our knowledge of the conditions necessary for the establishment of plants from seed has hitherto been inadequate.

The information set out below will assist in the better understanding of the factors controlling germination and seedling establishment, and at the same time the paper will discuss some of the ecological peculiarities of this group of halophytic plants.

Distribution and Habit of the Species Investigated

The five most widely distributed and economically important species of *Atriplex* [2] in Australia are *A. nummularia* (old man saltbush), *A. vesicaria* (perennial or bladder saltbush), *A. semibaccata* (creeping saltbush), *A. inflata* (halimus or flat-topped saltbush), and *A. spongiosa* (pop saltbush). The first four of these species occur within the 16-inch isohyet, extending into the most arid areas where the mean annual rainfall is about 5 inches. *A. semibaccata,* on the other hand, though it occurs commonly in the driest areas, is also found in small quantities near the eastern coast where the mean annual rainfall exceeds 30 inches.

The first three species mentioned above are perennials. *A. nummularia* reaches a height of 10 feet and about the same diameter. *A. vesicaria* forms small bushes some 2 to 3 feet in height. *A. semibaccata* is either prostrate, producing mats over the soil surface, or grows into small erect bushes about 2 feet high; the latter form only has been investigated. *A. inflata* and *A. spongiosa* are annuals; both form small hemispherical bushes about 2 feet high.

Anatomy of the False Fruits

The female flower of *Atriplex* has no perianth, protection being provided by two bracteoles. The ovary contains a single ovule. After fertilisation the two

[1] Much of the work included in this paper was done while the writer held the position of Research Officer and Botanist, Soil Conservation Service of New South Wales.

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[2] Terminology as in Black (1948).

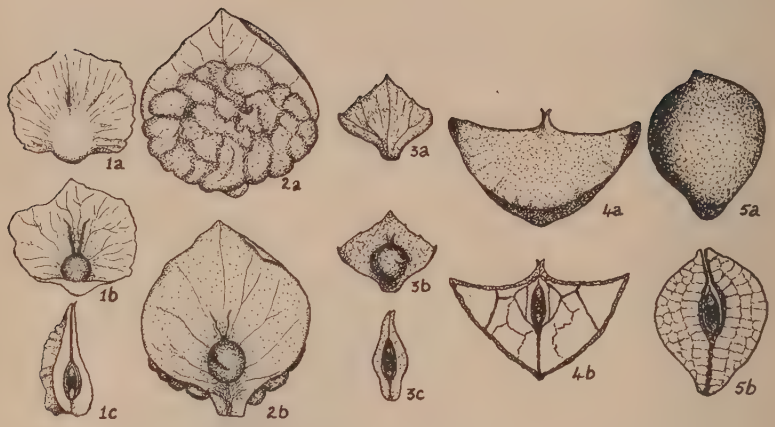

FIG. 1. Showing the structure of the false fruits of five species of *Atriplex* × 2. 1: *A. nummularia*. a. the false fruit; b. with one bracteole removed to show the true fruit; c. section through the false fruit at right angles to the bracteoles, showing the membranous pericarp and the seed. 2: *A. vesicaria*. a. the false fruit; b. with one bracteole removed. 3: *A. semibaccata*. a. the false fruit; b. with one bracteole removed; c. section through the false fruit at right angles to the bracteoles. 4: *A. inflata*. a. the false fruit; b. section through the false fruit at right angles to the bracteoles. 5. *A. spongiosa*. a. the false fruit; b. section through the false fruit at right angles to the bracteoles. Note the large air cavities in 4b and 5b.

bracteoles enlarge and enclose the fruit. The false fruit so formed (hereafter referred to as the "fruit") varies in shape and size according to the shape and size of the bracteoles (Fig. 1). In *A. nummularia* and *A. semibaccata* these bracteoles are leathery and closely appressed against the fruit; they are fused at the base only. In *A. vesicaria* the dorsal portion of each bracteole becomes spongy and is filled with air; the two bracteoles are fused near the base. In *A. inflata* and *A. spongiosa* the two bracteoles fuse completely, except at the very summit where a small aperture is left, too small to allow the seed to escape; the bracteoles at maturity are spongy and filled with air. The pericarp of all species is membranous and free from the seed; owing to its very delicate nature it is usually fragmented or even removed completely when the seeds are extracted from the bracteoles. The seeds are lenticular in shape, about 1 mm. thick and of various diameters and colours. In *A. nummularia* and *A. vesicaria* all seeds are grey-brown or brown and 1.5 to 2.0 and 1.5 to 2.5 mm. diameter respectively. In the remaining three species the seeds vary in colour and size within the species, and even on a single bush. In *A. semibaccata* and *A. inflata* some seeds are light brown and about 2 to 2.5 mm. diameter, while others are dark brown to black and about 1.25 to 1.5 mm. diameter; the two kinds of seed can be separated without difficulty. In *A. spongiosa* every gradation of colour and size occurs from black seeds 1 mm. diameter to light brown seeds 2.5 mm. diameter; it is impossible to separate the seeds into two well defined classes on the basis of colour and size. The colour of the testa is correlated with its permeability to water. Light coloured testas are freely permeable, and the seeds are referred to as "soft." Dark coloured testas are impermeable to water when the seed is shed from the plant; such seeds are referred to as "hard." This difference in the permeability of the testa has not been recorded previously in Australian species of *Atriplex*. Hard seeds have been noted in at least one other member of the Chenopodiaceae, namely, *Chenopodium album* by Rees (1910).

Incidence of Seeds in the "Fruits"

All "fruits" do not contain fully developed seeds (Table I). Since undeveloped ovaries are common, lack of seed is attributed in most cases to the fact that fertilisation has probably not taken place: the bracteoles apparently mature whether fertilisation takes place or not. The lowest incidence of seed is found in *A. nummularia* whose female flowers are borne in clusters of some hundreds. The condition is extreme during the first seeding of a bush and on isolated bushes. Malformation of the embryo is not uncommon and occurs most frequently in *A. semibaccata*. The cause is not known; insufficient water cannot be suspected as the cause since "fruits" from irrigated plants grown under cultivation commonly contain the highest percentage of malformed seeds. Destruction of the seed before maturity by insect larvae is quite common, and during storage this factor is responsible for damage to the seed, particularly in *A. inflata*. The ratio of light coloured to dark coloured seeds in those species where such a difference in colour occurs likewise varies from sample to sample (Table I).

Germination of Naked Seeds

Preliminary laboratory tests using seeds enclosed by the bracteoles, as would be found in the field, gave extremely low percentage germinations; however when naked seeds were set down on wet filter paper they germinated rapidly and in large quantities. It therefore follows that the bracteoles retard germination. The inhibiting substance proved to be chloride accumulated in the bracteoles; its mode of action and possible ecological significance are discussed below. Before it was realised that chloride is the important factor, light, aeration, and pH were investi-

Table I. *Incidence of seed in the "fruits" of various samples of five species of* Atriplex

Species	Date of collection	Locality	Number of observations	Mean incidence of light-coloured (soft) seeds per 100 "fruits"	Mean incidence of dark-coloured (mainly hard) seeds per 100 "fruits"	Total	Percentage "fruits" containing malformed or no seeds
A. nummularia	vi-1940	Broken Hill[x]	4	73± 5.0	nil	73	27
	vi-1941	Broken Hill[x]	5	60± 2.7	nil	60	40
	1942	Seed firm	4	24± 9.7	nil	24	76
	v-1944	Condobolin[x]	4	62±11.5	nil	62	38
	i-1945	Condobolin[x]	7	52	nil	52	48
A. vesicaria	vi-1941	Broken Hill	5	44± 4.0	nil	44	56
	x-1943	Condobolin[x]	3	97± 2.3	nil	97	3
	ix-1944	Condobolin[x]	5	98	nil	98	2
A. semibaccata	v-1940	Condobolin	4	69± 3.9	18±5.3	87	13
	v-1942	Condobolin[x]	6	45± 6.7	38±8.9	83	17
	v-1944	Condobolin	4	68± 2.6	6±2.9	74	26
	ii-1946	Condobolin[x]	1	11	84	95	5
	v-1946	Condobolin	6	72± 6.5	7±2.0	79	21
A. inflata	vi-1940	Broken Hill	3	57± 2.6	15±3.7	72	28
	iv-1942	Condobolin[x]	9	28± 4.6	33±4.6	61	39
	x-1943	Booligal	3	33± 1.5	6±1.0	39	61
	ii-1946	Condobolin[x]	5	40± 2.5	46±3.7	86	14
	v-1946	Condobolin[x]	4	26± 7.9	64±9.0	90	10
A. spongiosa	ii-1941	Bourke	3	*	*	93±3.5	7
	v-1942	Condobolin[x]	3	*	*	84±7.9	16
	xi-1943	Condobolin[x]	5	*	*	90±4.8	10

[x] Cultivated under irrigation.
* Cannot be estimated accurately owing to the gradation of colour.

gated. Since these three factors are relatively unimportant, only a descriptive summary of the results is given. In addition to these investigations the effect of temperature on the germination of naked seeds and the longevity of stored seed were studied in some detail.

The tests described in this section were made with naked seeds, either on wet filter paper in Petri dishes, or in soil. The seeds frequently had whole or part of the pericarp attached; the latter, however, being extremely thin does not affect germination in any way. For the tests done in Petri dishes the emergence of the radicle was taken as the criterion for successful germination; for the tests done in soil the emergence of the cotyledons above soil level was taken as the criterion. For each test 100 seeds were used, except for the tests at different pH values where 50 seeds only were used for each test.

The effect of light

Soft, naked seeds of each of the five species lying on wet filter paper in the dark and in diffuse sunlight at room temperature (15–20° C) gave comparable germination percentages. Light apparently has no effect either in accelerating or retarding germination; the bracteoles therefore have no significance as far as light is concerned. Field evidence, both experimental and under natural conditions, to support this conclusion is abundant: seeds enclosed within the partly decayed and fragmented bracteoles germinate freely if well watered, both when buried in the soil and lying on the surface in direct sunlight.

The effect of pH

When the seed is mature on the plant and the bracteoles are still green the pH of the cell sap of the bracteoles lies between 5 and 5.5. As the bracteoles dry out the sap becomes less acid, and when airdry the water extract of the bracteoles has a pH value of 8 to 9. When bulk samples are collected "fruits" of various degrees of dryness are invariably taken, and at one stage in the work premature picking of the fruits was suspected as the cause of retarded germination in so far as the acid cell sap may reduce the permeability of the testa to water. Two experiments were carried out to investigate this point:

Firstly, green and dry "fruits" were collected from the plants and stored separately. The pH of the cell sap of the green "fruits" was measured daily; as the "fruits" dried out the pH rose steadily to a value of 8. When dry, samples of seeds were removed from the two sets of "fruits" and put down on wet filter paper to test for germination capacity. Both sets of seed gave similar results.

Secondly, soft seeds of the five species were put down on filter paper saturated with McIlvaine's (1921) phosphate-citrate buffer solutions diluted with five volumes of water to give solutions whose osmotic pressures were too low to interfere with germination (see below where germination in salt solutions is discussed). The pH values ranged from 3.0 to 8.0 at intervals of one pH unit. The trials were carried out at room temperature. The seeds of all five species gave comparable germination percentages at all pH values used. The figures, however, have little significance since the seed, by means of its buffer systems, adjusts the pH of the most acid solutions to about pH 6 outside the testa.

The results of these two experiments give ample proof that pH has no significant effect on the permeability of the testa as far as germination is concerned; also that germination occurs over a wide range of pH. Furthermore, pot experiments carried out in Sydney have shown that all five species can grow satisfactorily and that the two annual species produce seed in soils whose pH is as low as 5.5, which value is lower than that of any of the soils in which *Atriplex* is found naturally.

The effect of aeration

Germination can be prevented by surrounding the seeds by films of water. The inhibition is apparently caused by an insufficency of oxygen. That carbon dioxide is not the limiting factor under conditions of waterlogging (for example when the seed is enclosed in the water-saturated bracteoles, see below) was demonstrated by the following rough quantitative test. Soft naked seeds of the five species were sown on wet filter paper in bottles filled with air containing approximately 4% carbon dioxide. Germination proceeded at 20° C at rates similar to those obtained from seed on wet filter paper in the atmosphere. At the same time a rough estimate of the carbon dioxide in "fruits" which had been waterlogged for one week gave an approximate carbon dioxide concentration of less than 1%. This figure was obtained by mixing waterlogged "fruits" with standard baryta, followed by back titration of the residual alkali with standard acid. Waterlogging for a period of three weeks does not harm the seeds, which germinate satisfactorily when removed from the waterlogged environment and placed on a moist medium in contact with the atmosphere. Field observations confirm this point: flooding of river flats and depressions is a common occurrence after rains, and as the water recedes zones of *Atriplex* appear in the moist soil even though the seed has been waterlogged for weeks.

The effect of temperature

Soft seeds of all five species germinate at temperatures between 0 and 35° C (Table II). Above 25° C the percentage

TABLE II. *Percentage germination of seeds of five species of* Atriplex *at various temperatures. Only soft seeds were used in the tests, except for* A. spongiosa *in which it is impossible to sort soft and hard seeds by eye. For this species mixed seed about 2 years old was used; at the end of 21 days the hard seeds (then ungerminated) were pricked. The total percentage germination of hard and soft seeds is given after 28 days*

Temperature °C	Percentage germination															
	A. nummularia			*A. vesicaria*			*A. semibaccata*			*A. inflata*			*A. spongiosa*			
	2 days	7 days	21 days	2 days	7 days	21 days	2 days	7 days	21 days	2 days	7 days	21 days	2 days	7 days	21 days	28 days
0	0	0	5	0	0	79	0	0	80	0	0	76	0	0	28	28
5	0	20	96	0	56	100	0	76	100	0	80	96	0	26	59	61
10	2	78	97	0	96	100	8	100	100	0	85	97	4	48	91	100
15	7	88	100	0	99	100	29	100	100	14	90	100	14	37	77	100
20	19	84	86	9	95	100	12	89	100	15	93	95	26	78	85	100
25	24	97	100	8	95	100	12	60	90	39	95	100	11	43	84	100
30	10	19	24	12	20	37	13	38	52	0	42	60	25	37	39	51
35	0	0	10	0	0	9	12	25	25	2	2	26	8	8	14	14
3 hours at 35° C, 21 hours at 20° C	13	100	100	8	100	100	52	100	100	46	96	96	18	80	83	100
6 hours at 35° C, 18 hours at 20° C	21	100	100	6	93	100	42	100	100	20	72	81	30	80	86	100

TABLE III. *Percentage germination of seeds of five species of* Atriplex *at various times after shedding. For dark coloured seeds two figures are given in each column: the top indicates the percentage of seeds whose testas become permeable naturally; the lower figure indicates the total percentage germination after any remaining hard seeds have been pricked. The difference between the two figures therefore represents the percentage hard seeds present*

Species	Type of testa	Percentage germination after various times (in years)								
		0	1	2	3	4	5	6	7	8 years
A. nummularia	light-coloured (soft)	92	90	—	—	76	62	44	12	10
A. vesicaria	light-coloured (soft)	92	80	71	51	10	0			
A. semibaccata	light-coloured (soft)	66	44	3	0					
	dark-coloured unpricked	0	76	84	80	86	90	71	16	6
	dark-coloured total	100	100	100	80*	86*	90*	71*	16*	6*
A. inflata	light-coloured (soft)	100	100	—	85	82	31	0		
	dark-coloured unpricked	3	74	78	65	—	70	28	12	0
	dark-coloured total	100	100	100	100	—	100	28*	12*	0
A. spongiosa	soft and hard mixed unpricked	26	67	83	85	96	76	43		
	soft and hard mixed total	100	100	100	100	100	76*	43*		

* Indicates absence of hard seeds.

germination decreases; at 35° C radicles sometimes emerge but are soon killed. Considering only the total percentage germination after 21 days, the temperature for full germination of each species is very wide: 5–25° C for the first four species and 10–25° C for *A. spongiosa.* If both rate and amount of germination be considered, the optimum temperatures are 20–25° C for *A. nummularia* and *A. vesicaria,* 15° C for *A. semibaccata,* 25° C for *A. inflata,* and 20° C for *A. spongiosa.* These figures are similar (though the ranges are somewhat wider) to those quoted by Burbidge (1945) and Trumble (1932) for *A. vesicaria* and *A. semibaccata* respectively. Short exposures to 35° C for 3 and 6 hours per day, which conditions obtain in the field during the summer months, do not have any effect on the rate or amount of germination if the temperature for the remainder of the 24-hour period falls within the germination range (Table II).

The embryos of hard seeds react to temperature in the same way as do those of soft seeds. The permeability of the hard testas is not increased by subjecting seeds in the moist condition to a continuous temperature of 35° C for a period of 3 weeks. Since such high wet soil temperatures are not experienced for this period even during extremely hot summers, hard seeds are not softened by the environment.

Longevity of the seed

Samples of each of the five species collected between 1940 and 1946 in various localities were tested annually for viability over a period of up to 8 years. Selected sets of figures showing the percentage germination of the seed of the five species at various ages are given in Table III.

The longevity of soft seeds varies from species to species and is not related to the life-span of the plant: for example, soft seeds of *A. semibaccata,* a perennial, have a shorter life than the soft seeds of *A. inflata,* an annual; on the other hand, soft

seeds of *A. nummularia,* a perennial, have the longest life of all.

Hard seeds live for longer periods than do soft seeds of the same species. The permeability of the testa of hard seeds increases with time: after the first year 65–75% of the hard seeds are permeable (Table III), and thereafter a small percentage becomes permeable each year. All seeds are capable of absorbing water after three years in the case of *A. semibaccata,* 5 years in the case of *A. spongiosa,* and 6 years in the case of *A. inflata.*

It is difficult to evaluate the importance of the hard seed. Theoretically it appears advantageous, and field observations made over a period of 10 years give evidence of the steady replacement of the two perennials that lack hard seeds by the two annuals that possess hard seeds. Whether the hard seed is responsible for this change or whether some other factor such as the rapid seed production, even under conditions of scant water supply, or the drought-evading properties of the annuals is responsible, is difficult to estimate.

Of significance is the fact that hard seeds which cannot germinate immediately after shedding are less liable to be destroyed by small showers of rain than are soft seeds. (It may be mentioned here that the latter have a temporary protective mechanism afforded by the bracteoles and their included chloride; this is described below.) Consequently hard seeds probably accumulate in the soil and on the surface as a reserve supply that becomes available when the testas become permeable. A certain amount of field evidence in support of this has been collected: mats of seed that have been lying under bushes for some months invariably contain very high percentages of hard seeds; in some cases only hard seeds can be recovered from such mats, and when this is so many empty bracteoles are also to be found. It is assumed that the empty bracteoles contained soft seeds which were destroyed by small falls of rain that were large enough to germinate the seed, but inadequate for the establishment of the seedling. There is no doubt that enormous quantities of seed, both soft and those hard seeds whose testas have become permeable, are lost every year after small showers of rain. Mats of dead seedlings, usually in the cotyledon stage, are commonly found, particularly during drought periods and during the warmer months of the year. Thus it is probable that over a period of years ineffective falls of rain lead to a depletion in the supply of soft seeds, and, in areas where mature bushes that could replenish the supply have been removed either by stock or by drought, seed for regeneration is completely lacking. This is the case for vast areas of former perennial saltbush country. Proof that a lack of viable seed is preventing regeneration of soft seeded species is supplied by the enclosure of small areas against stock after which no seedlings appear even after periods of up to 10 years. On the other hand, when seed is sown in adjacent enclosures seedlings appear in large numbers (unpublished data).

Germination of the Seed Enclosed in the Bracteoles

When the seed is first shed from the plant it is enclosed in the bracteoles and remains enclosed unless the bracteoles decay or are removed by abrasion. Partial removal by abrasion following desiccation is common in *A. spongiosa* and *A. inflata* and occurs occasionally in *A. vesicaria.* In the remaining two species the entire bracteoles usually persist long after the seed has lost its viability.

When enclosed by the bracteoles the seed germinates only after relatively long periods when the "fruits" are set down on wet filter paper (Table IV, and compare rates of germination in Table II). The retardation is caused by high concentrations of chloride ions (Table V) that must be partially removed in order to give solutions of sufficiently low osmotic concentration to permit germination. The rate of salt removal from the dry "fruit" by diffusion is governed partly by the shape of the bracteole and the arrangement

TABLE IV. *Percentage germination of soft seeds enclosed by the bracteoles under three moisture treatments. Tests done at 20±4° C. For further explanation, see text*

Species	Percentage germination								
	Dry "fruits" on wet filter paper			"Fruits" soaked for 24 hours and the excess water removed			"Fruits" waterlogged		
	2 days	7 days	21 days	2 days	7 days	21 days	2 days	7 days	21 days
A. nummularia	0	15	70	0	2*	76	0	0	1
A. vesicaria	0	14	24	0	54	81	0	0	4
A. semibaccata	3	84	100	4	100	100	0	0	0
A. inflata	0	28	38	26	88	92	0	0	9
A. spongiosa	0	0	6	0	42	100	0	1	16

* Suppression of germination (compare dry "fruit" figure) is apparently caused by temporary waterlogging.

of the enclosed air spaces. Thus the flat bracteoles of *A. nummularia* and *A. semibaccata* that present a proportionately larger surface to the wet filter paper than do the rounded bracteoles of the spongy types permit of the more rapid germination (Table IV). Furthermore, the large amount of air space in the spongy types (Fig. 1) which limits the area of tissue capable of providing a diffusion path for the chloride is an additional factor retarding germination in these types; this is of greatest significance in *A. spongiosa*.

The amount and rate of germination are readily increased by reducing the chloride concentration by soaking the "fruits" in water. Any period of soaking suffices, provided all the excess water is removed from the "fruits" (e.g. by squeezing between blotting paper) to prevent waterlogging of the seed. A typical set of figures to illustrate the effect of soaking is

TABLE V. *The amount of chloride, expressed as NaCl, in the bracteoles of five species of* Atriplex *and its relationship to the absorption of water, together with the molar concentration developed in the bracteoles when fully absorbed, and the molar concentration of NaCl required to prevent germination of the seed*

Species	Date of collection of seed	Locality	Percentage NaCl in oven-dry bracteoles	Percentage water absorbed by oven-dry bracteoles after 9 days in a saturated atmosphere at 20° C	Molar concentration of NaCl in saturated bracteoles	Molar concentration of NaCl required to prevent germination
A. nummularia	iv–1944	Condobolin*	11.1	264	0.72	0.6
	iii–1946	Broken Hill*	1.8	63	0.48	0.4
A. vesicaria	vi–1944	Condobolin*	7.4	265	0.48	0.4
	x–1943	Condobolin*	5.3	164	0.55	0.5
A. semibaccata	v–1944	Condobolin	10.2	284	0.61	0.4
	i–1947	Condobolin	3.9	150	0.45	—
A. inflata	v–1947	Wilcannia	31.1	593	0.90	0.7
	iv–1942	Condobolin*	10.5	292	0.61	0.5
	x–1943	Oxley	7.4	283	0.44	0.4
	v–1946	Condobolin	6.3	192	0.56	—
A. spongiosa	v–1947	Wilcannia	11.8	325	0.62	0.6
	v–1942	Condobolin*	7.3	182	0.69	0.4

* Cultivated under irrigation.

given in Table IV. These figures have been selected to illustrate an additional point, namely, the retardation of germination caused by temporary waterlogging as a result of incomplete removal of water from the bracteoles (see figures for *A. nummularia*). This temporary waterlogging occurs most frequently under laboratory conditions in the flat bracteole types. The point is mentioned since his explanation reasonably accounts for the retardation, which initially led to some confusion. The effect of complete waterlogging under laboratory conditions is shown in the third set of figures in Table IV. Experiments done in waterlogged soil also indicated that waterlogging suppresses germination; actually no germination whatsoever was recorded for any species in the waterlogged soils.

The retarding effect of the accumulated chloride ions is interpreted by the writer as a mechanism that protects the seed, in particular soft seeds (hard seeds already having a protective mechanism), against germination during climatic periods unfavourable to seedling establishment. The mechanism is undoubtedly only temporary but it is possibly very effective under certain climatic conditions. Field observations and laboratory experiments to support this contention are given below.

When the "fruits" are shed from the plant they accumulate along with dead leaves below the parent. The mat of "fruits" and leaves is a hygroscopic mass of colloidal material impregnated with chloride. The amount of chloride, to which the hygroscopicity is largely attributable, varies considerably within species and from species to species (Table V). In humid atmospheres the bracteoles absorb water, the amount absorbed being a function of the chloride content (Table V and Fig. 2). When the concentration of the chloride in the bracteoles is high (5 p.c. or more of the dry weight) absorption is so great that globules of solution are exuded from the surface of the bracteoles. However, even when the bracteoles have absorbed as much water as they can from the saturated atmosphere, no germination occurs. Failure to germinate is due to the fact that the concentration of salt solution held in the bracteoles is higher than the concentration permitting germination. This has been confirmed by estimating the percentage germination of naked seeds lying on pads of filter paper saturated with sodium chloride solutions of various molar concentrations. In each case it was found that the percentage germination decreased as the concentration of salt increased. In all cases 0.2M NaCl does not appreciably suppress germination, whereas 0.3 M NaCl reduces the germination to about 20% of the expected germination in a salt-free medium. Higher concentrations cause a greater suppression, to values of

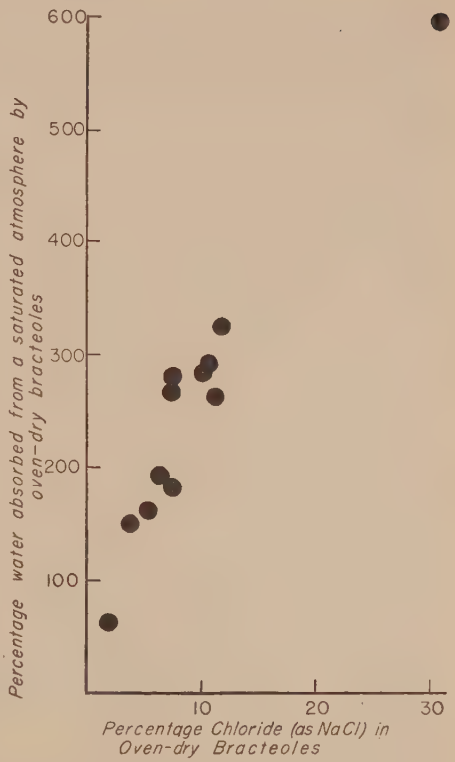

FIG. 2. Showing the relationship between water absorption and salt concentration in the bracteoles of *Atriplex*.

about 5%, while the concentration of salt required to suppress germination completely is invariably lower than the concentration developed in the fully absorbed bracteoles (Table V).

There is little doubt that protection occurs but it is effective only for falls of moisture (either dew or rain) that do not percolate through the mass of "fruits" and leach away some of the chloride. Field observations suggest that in most years protection is removed within a year from seed-shedding. Perhaps during times of drought the period may extend into the second year, and in this respect it is relevant that viable seeds of *A. vesicaria* which are obviously from the previous year's crop have been recovered from the ground.

Further evidence of temporary protection is given by a series of pot experiments designed to ascertain the amount of water required to germinate the seeds and establish the seedlings. These experiments were set up at Condobolin, some 280 miles west of Sydney. Though not lying within the true saltbush area the climate is very similar to that of the saltbush country, and two of the species, *A. nummularia* and *A. semibaccata,* occur in the district as members of the shrub layer of the *Eucalyptus* woodlands. The trials were set up as follows.

Forty-five 4-gallon containers were filled with a sandy loam soil and "fruits" of the five species of *Atriplex* were sown on the surface and lightly covered with soil. The number of "fruits" sown in each container varied from 30 to 100, according to the soft seed content of the sample. Three irrigation treatments were applied, the equivalents of 1, 2 and 3 inches of rain in one fall. Each water treatment was triplicated for each species. No more water was given for the duration of the experiment, the pots being covered by canvas blinds when rain threatened. An additional set of "fruits" was sown in separate pots as a control; these were watered when necessary to keep the soil moist. The observed germinations of these sowings were taken as a measure of the germination capacity of the sample; the germinations in the other

TABLE VI. *Germination of soft seeds in soil under three rainfall treatments. For further explanation, see text*

Species	Water treatment (inches of "rain")	Percentage germination			
		Summer conditions (mean max. temp. 36° C, mean humidity 28%)	Winter conditions (mean max. temp. 15° C, mean humidity 62%)		
		10 days	10 days	21 days	35 days
A. nummularia	1	0	0	24	24
	2	0	0	50	64
	3	4	0	36	59
A. vesicaria	1	0	0	87	87
	2	0	0	83	83
	3	6	0	85	100
A. semibaccata	1	0	2	25	31
	2	3	3	36	53
	3	7	10	66	75
A. inflata	1	0	0	62	62
	2	0	5	58	58
	3	1	16	100	100
A. spongiosa	1	0	14	69	69
	2	0	21	73	79
	3	0	58	100	100

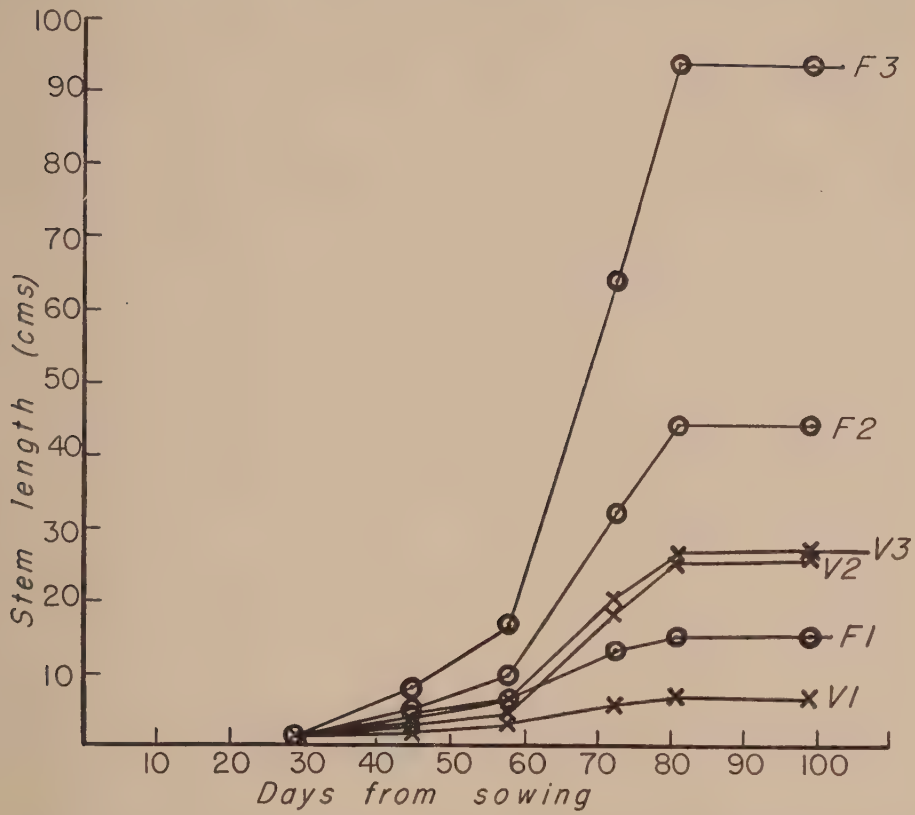

FIG. 3. Growth curves of *Atriplex* seedlings under three different water treatments. Symbols: V = *A. vesicaria;* F = *A. inflata.* The figures following these letters indicate the amount of rain in inches supplied to the containers.

containers are expressed as percentages of these control figures.

Four of these trials were laid down over a period of three years, in January, May, June, and August. Daily observations were made during the early part of the experiment, the number of cotyledon pairs being recorded. The results of a summer and a winter trial are given in Table VI. In the summer trial what germination occurred was complete within 10 days; in the winter trial it extended over a period of five weeks, though most of the seed germinated within three weeks after wetting. The marked difference between the percentage germinations in the summer and winter is due to the rapid drying out of the summer trial. In this trial the surface of the soil of the one-inch treatment was dry within 24 hours, while the seed had dried out within 2 days; in the 3-inch treatment the seed remained moist for 6 to 7 days. Since the seedlings were required for further observation, it was not convenient to deal with the ungerminated seed quantitatively. However, representative samples were recovered and tested for viability. Of the two viable seeds recovered from the winter trial, both were hard. On the other hand, much viable soft seed was recovered from the summer trial; on testing for viability, seeds removed from the bracteoles germinated freely while those set down enclosed within the bracteoles showed the usual germination lag indicating that the

TABLE VII. *Total stem length, survival period, and seed production of seedlings grown under three different water treatments during the summer and the winter (for climatic data, see Table VIII)*

Species	Water treatment (inches of "rain")	Summer grown		Winter grown		
		Total stem length (cms)	Survival period (days from sowing)	Total stem length (cms)	Survival period (days from sowing)	Number of viable seeds produced
A. nummularia	1	*	—	3± 1	104	nil
	2	*	—	10± 3	114	nil
	3	1	15	20	120	nil
A. vesicaria	1	*	—	6± 3	100	nil
	2	*	—	26±10	100	nil
	3	2	15	26± 1	112	nil
A. semibaccata	1	*	—	10± 2	92	nil
	2	3	15	61±13	109	nil
	3	3	15	59±14	113	nil
A. inflata	1	*	—	16± 6	102	nil
	2	*	—	44±21	100	nil
	3	2	15	94± 9	103	nil
A. spongiosa	1	*	—	27±10	100	12
	2	*	—	45± 6	98	29
	3	*	—	45	103	31

* No germination.

inhibiting action of the salt was still operative, and in this case had protected the seed against unsuccessful establishment.

WATER REQUIREMENTS FOR THE ESTABLISHMENT OF THE SEEDLINGS

The seedlings in the containers mentioned above were allowed to continue growth, and when the first pair of leaves had expanded all but the largest seedling were removed from each pot. The total stem lengths of these plants were measured from time to time until the plants died. Typical growth curves are given in Figure 3, for *A. vesicaria,* a perennial, and *A. inflata,* an annual. A summary of the data for all five species is given in Table VII, and relevant climatic data for the growing periods are given in Table VIII. Of interest are the following points:

(a) There is a marked difference in the size and the survival periods of plants grown during the summer and winter. This is due primarily to differences in the rates of atmospheric evaporation. The summer-grown plants produced only

TABLE VIII. *Climatic data for the periods over which the growth trials in Table VII were conducted*

	Summer trial	Winter trial							
	14-i-42 to 30-i-42	23-viii-43 to 6-ix-43	7-ix-43 to 21-ix-43	22-ix-43 to 6-x-43	7-x-43 to 21-x-43	22-x-43 to 5-xi-43	6-xi-43 to 20-xi-43	21-xi-43 to 5-xii-43	6-xii-43 to 12-xii-43
Mean max. temp. ° C	37.2	13.3	16.6	19.5	23.2	25.6	23.0	25.6	28.7
Mean percentage humidity (2 p.m.)	25	63	61	55	39	36	38	29	34

cotyledons and a stunted pair of mature leaves. No more need be said about the latter plants. Unless otherwise stated the remarks that follow refer to the winter-grown plants only.

(b) The amount of growth produced by a single inch of rain is least for the robust perennials and most for the annuals. Doubling the amount of water more than doubles the amount of growth, but the third inch of rain does not appear to produce a proportionate amount of growth (except in *A. inflata*). No further conclusions can be drawn from the figures since the small number of replicates, especially for *A. nummularia* and *A. spongiosa* where seedlings were lost through damage by birds, renders the data inadequate.

(c) Of greatest significance is the fact that all of the seedlings, irrespective of the amount of water received, survive for approximately the same period. Furthermore, a survival period of 100 days, especially for the one-inch treatment, appears to be extraordinarily long. In this respect it is relevant to mention here that the survival period of seedlings from seed sown earlier in the winter (June) are probably much longer than those quoted above. The trial set down in June unfortunately had to be discarded because an unexpected heavy fall of rain rewet the unprotected plants. The plants, however, after a period of 105 days had grown larger (apparently because of the warmer conditions during the early part of the growing period) than those referred to in Table VII. By comparing the growth curves of the two sets of seedlings a survival period of 140 days at least is estimated for the June-sown trial.

No comparative data for the survival periods of other plants are available. However, from semi-quantitative observations made over a period of years on crop plants and non-halophytic annuals and perennials in the semi-arid country, a survival period of 100 days is most unexpected. Some indirect evidence to support this contention is supplied by the data of Miller (1947) who, using the observed climatic data, calculates that under the conditions prevailing at the time of the experiments wilting point of the soil for the 3-inch treatment should be reached after a period of 46 days, for the 2-inch treatment after a period of 33 days, and for the one-inch treatment after a period of 18 days. These survival periods are of the same order as the survival periods observed by the writer for crop plants grown in the Condobolin district. Furthermore, Miller's calculated figure for the soil to reach wilting point under the summer trial climatic conditions is 21 days for the 3-inch treatment and 14 days for the 2-inch treatment, which agree fairly closely with the observed figure of 15 days. These data introduce an interesting point which is at present under investigation and will form the subject of a subsequent paper: the long survival period during the winter months when humidities are high and dews are common may be related to the power of the leaves to absorb atmospheric moisture by virtue of their high chloride content. This theory has already been put forward by Wood (1925) though there is as yet no experimental evidence to support it.

The data have also a practical application: sowing of *Atriplex* seed for regeneration purposes should be done during the winter months, when good germination can be expected, provided the seed is sown in wet soil. Sowing after a fall of one inch will produce seedlings whose anticipated life from the single inch is of the order of 100 days. Moreover, climatic data indicate that during any 100-day period during the winter the expectation of a following rain is extremely high. Seedling establishment is therefore not difficult under selected winter conditions (in stock-free areas), a fact that has been substantiated for *A. nummularia* and *A. inflata* at Condobolin (unpublished data).

(c) The two annual species have as long a survival period as the three perennials. If survival period is a measure of drought resistance, then the annuals are

not only drought evaders, but at least as drought resistant as the perennials.

(d) The water requirement for the production of seed is lower for *A. spongiosa* than for *A. inflata*. The abundance of seed of *A. spongiosa* in the field after rains and the appearance of this species only in time of drought in depressions in a stunted but fruiting form after falls of less than one inch of rain lend support to this view. (That this difference is due to water requirement rather than a photoperiodic effect is supported by the fact that seed of both species can be collected at all times of the year.)

Summary

The germination of the seeds of five Australian species of *Atriplex* under various conditions, and the behavior of the seedlings under three irrigation treatments are discussed.

Three of the species have hard seeds, the percentage of which varies from sample to sample. Soft and hard seeds react similarly to external conditions, except in so far as the hard testa retards the uptake of water. Hard seeds become permeable after a few years.

Both soft and hard seeds germinate equally well in the dark and in the light, and over a wide range of pH. For successful germination the seeds must be in contact with the air, and not surrounded by films of water. All species germinate over a wide range of temperature.

The life of soft seeds varies from species to species and is not associated with the life span of the plant; hard seeds remain viable for longer periods than do soft seeds of the same species. The hard seed appears to be an advantage ecologically and is possibly responsible for the replacement of soft-seeded perennials by annuals that possess hard seeds.

The bracteoles that envelop the seed contain high percentages of chloride which renders them hygroscopic. The chloride retards, and under certain conditions inhibits, germination. Its presence is interpreted as a mechanism which leads to the protection of the seed against unsuccessful establishment during climatically unfavourable periods.

Seedling establishment can be effected with a scanty water supply during the cooler months of the year; a single inch of rain in one fall is sufficient to establish seedlings of all species. Seedlings of all species survive for extraordinarily long periods. The size of the seedling is governed by the initial amount of water provided, but the survival period is independent of this. The long survival periods may be related to the ability of the plant to absorb and utilise atmospheric moisture either as vapour or in the form of dew. This property is possessed by both annuals and perennials and consequently the annual species appear to be as drought resistant as the perennials.

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THE RELATIONSHIP OF NEST PROTECTION AND HUDDLING TO SURVIVAL OF PEROMYSCUS AT LOW TEMPERATURE [1]

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It seems obvious that the degree of protection offered by nests during winter must be an important factor influencing the survival of small mammals during periods of extreme cold when they are not actively searching for food. Absence of suitable nesting material, lack of natural hiding places, or inability to burrow below the surface would allow the full effect of low temperature to be exerted more drastically and might well be major factors contributing to winter mortality in the absence of other protective mechanisms. Although the protection afforded by the nest probably prolongs survival at all temperatures below that of thermal neutrality its effectiveness is perhaps greatest at extreme low temperatures when prevention of excessive heat loss is most vital for conserving energy reserves. Huddling of mice in groups of two or more individuals must also play a not inconsiderable part in prolonging survival at low temperatures. When combined with nest protection the resistance to low temperature might be enhanced still more by a summation effect.

Richter (1942) reported that thyroidectomized or hypophysectomized rats, which have limited physiological means of maintaining normal body temperature, build large nests in an attempt to conserve their heat. He also emphasizes (Richter 1927) the importance of other thermo-regulatory activities of the rat such as burrowing, huddling into small spaces, and huddling together in conserving body heat.

In a study of nest-building activity of the albino rat, Kinder (1927) exposed groups of rats to outdoor temperatures from 40–60° F. and to indoor temperatures of around 90° F. and found that nest-building appeared more promptly at moderate or low temperatures than at high temperatures. Decided differences in temperature not only influenced the time of appearance of the activity, but also entirely changed the level of activity which had already been established. Thus, animals accustomed to building large nests at low outdoor temperatures practically ceased this activity when removed to a heated room, while the nest-building of rats acclimated at high temperature was enormously increased when they were placed outdoors.

In a study of the cottontail (*Sylvilagus floridanus mearnsii*) in southern Michigan (Linduska 1947) it was found that "holing up" by rabbits was not dependent upon any critical temperature but underwent a gradual increase with lowering temperatures. Den occupancy by rabbits at minimum daily temperatures of −8° to 12° F. was about three times that found on days when the minimum temperatures were between 13° and 32° F. Whitney (1931) working in Massachusetts and Connecticut found that raccoons were inactive on colder nights, "holing up" with a drop in temperature and becoming active with a rise in temperature, during both fall and winter. The same reduction in activity of raccoons during colder weather was noted by Steuwer (1943) in Michigan.

The relationship of nest protection to survival of small mammals at low temperatures has apparently never been investigated in a quantitative way. Cory (1912) in a discussion of the winter habits of *Microtus pennsylvanicus* comments in a general way on the importance of the

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nest as a means of protection from the cold. Others have frequently assumed a considerable protective value for the nest during periods of cold weather without making any actual measurements of the degree of protection offered. Thomsen (1945) in a study of the winter habits of the northern white-footed mouse found that during the day his mice remained quiet, huddled in a corner of the cage, and assumed that they spend the day in their winter nest in similar huddles. Huddles are common among caged mice in the laboratory, and especially so when deprived of nesting materials at low temperature. No quantitative evidence is extant in the literature which would indicate whether or not such huddles prolong the survival time of mice exposed to low temperatures, although inferences which may be drawn from metabolism data (Brody 1945; Pearson 1947) point to such a relationship.

Materials and Methods

Wild deer mice used in the experiments reported here were as follows: The northern white-footed mouse, *Peromyscus leucopus noveboracensis,* the prairie deer mouse, *Peromyscus maniculatus bairdii,* and a deer mouse, *Peromyscus maniculatus austerus,* native to Washington. Specimens of *P. m. austerus* were obtained from B. T. Ostenson, Parkland, Washington, while the others were collected from wild populations in the vicinity of Champaign-Urbana, Illinois.

Animals designated as summer animals were taken between June 15 and September 15, while those individuals called winter animals were taken from November 15 to March 1 (Sealander 1951).

Survival times of huddling mice at very low temperatures were determined by direct observation at frequent intervals. The mice were exposed singly and in groups of two, three, and four individuals. Survival runs were carried out in complete darkness and in the absence of food and water. Survival times were determined individually for each mouse in a group, and the mean survival time for the group was determined by averaging the individual survival times.

Mice were immediately removed from each group when dead in order to prevent cannibalization of the carcass which would prolong survival time of the remaining mice. Both *noveboracensis* and *bairdii* showed a tendency toward cannibalism when deprived of food and water at low temperatures, but this type of behavior was not observed for *austerus.*

In the determination of survival times of huddling mice all individuals of *bairdii* and *austerus* were previously acclimated at temperatures ranging from about 19–22° C. in the laboratory for a period of approximately six weeks before undergoing the survival runs. Individuals of *noveboracensis* were used shortly after trapping from wild populations during the first half of April. Average temperatures in the field during this period were approximately equivalent to those temperatures at which *bairdii* and *austerus* were acclimated.

Survival time of *noveboracensis* provided with nest protection was determined by an indirect method utilizing thermocouples which was supplemented by direct visual observation at one- or two-hour intervals. The indirect method utilized the difference in temperature between a thermocouple recording air temperature in the cold chamber and another thermocouple placed within the nest or nest cavity which recorded the temperature near the animal (Sealander 1951).

The mice were subjected to air temperatures of $-30°$ C. and below while provided with nesting material in the form of a ball of cotton roughly the size of a golf ball, or while confined in a simulated wooden nest cavity containing either sawdust alone, or a natural grass and fiber nest constructed by *noveboracensis* under natural conditions. It is not intended to imply that cotton is similar to or has the same insulation value of natural nesting materials, but it was used solely to determine the effect on survival time of nesting material having definite insulating

value when natural nests could not be readily located.

The simulated nest cavity consisted of a wooden box having outside dimensions of 5 × 5 × 5 inches and constructed from ¾ inch pine lumber. A closely fitting cover fitted flush with the top of the box. Several small holes were drilled through the sides of the box to insure adequate ventilation, and a thermocouple was introduced into the box through another small hole to record temperature.

No food or water was provided any of the animals undergoing survival tests while provided with some form of nest protection.

Survival in Relation to Nest Protection

Data on survival time of freshly caught *noveboracensis* with nest protection are presented in Table I. Comparison of survival times of summer and winter animals under comparable conditions of temperature and insulation shows that in every case the winter animals were far more resistant to low temperature. The nest-building response as well as the type of nest built varied between winter and summer animals. It was observed that winter mice when put in the cold chamber immediately engaged in nest-building and within a relatively short time had made the most efficient use possible of the nesting material provided. Summer animals, on the other hand, neither responded to cold so rapidly nor with such pronounced nest-building instincts. In most cases the nests of summer animals were poorly constructed, open at the top or sides, and often consisted merely of a platform-like affair with a depression in the center. Usually more than a half-hour elapsed before the summer animals made other than sporadic attempts at nest-building.

Comparison of the survival time and the total per cent of initial weight lost at death by summer animals having nest protection with that of unprotected animals at the same temperature (Sealander 1951) shows that summer animals thus protected are able to prolong their survival time. Animals protected only very meagerly by a thin covering of cotton were apparently able to lower their rate of weight loss per hour but were unable to prolong their sur-

Table I. *The effect of nest protection on survival time of adult* P. l. noveboracensis *confined in complete darkness without food at low temperatures during summer and winter*

Sex	Mean air temperature (° C.)	Season	Survival time (hours)	Initial weight (grams)	Final weight (grams)	Per cent of initial weight lost	Nature of nest protection
F.	−32	Summer	1.6	24.9	24.7	0.80	Crudely constructed thin cotton nest, open at top
F.**	−32	Summer	1.5	29.3	29.1	0.68	Crudely constructed thin cotton nest, open at side
M.	−30	Summer	1.9	22.7	21.4	5.73	Poorly constructed cotton nest open at side and top
M.	−32	Summer	2.1	26.6	25.7	3.38	Poorly constructed cotton nest open at side and top
F.	−32	Summer	2.2	25.5	24.2	5.10	Poorly constructed cotton nest open at side and top
F.*	−32	Summer	1.3	33.6	33.2	1.19	Simulated nest cavity containing sawdust
M.	−33	Summer	1.2	22.7	22.5	0.88	Simulated nest cavity containing sawdust
M.**	−33	Summer	7.8	27.6	24.1	12.68	Simulated nest cavity containing natural grass and fiber nest
F.	−33	Summer	4.4	22.3	19.7	11.66	Simulated nest cavity containing natural grass and fiber nest
M.**	−32	Winter	29.0	29.0	20.2	30.34	Complete nest of cotton with no openings
F.	−32	Winter	18.0	22.0	16.0	27.27	Partial nest of cotton with small opening at top
M.	−32	Winter	15.6	22.2	18.0	18.92	Partial nest of cotton rather open at top
F.	−34	Winter	16.3	25.4	21.9	13.78	Simulated nest cavity containing sawdust
M.**	−34	Winter	7.3	30.9	28.9	6.47	Simulated nest cavity containing sawdust
F.	−35	Winter	50.3	25.2	18.3	27.38	Simulated nest cavity containing natural grass and fiber nest
F.	−35	Winter	23.7	27.2	23.6	13.23	Simulated nest cavity containing natural grass and fiber nest
F.	−35	Winter	31.9	23.5	18.2	22.55	Simulated nest cavity containing natural grass and fiber nest
F.	−35	Winter	45.6	24.3	17.2	29.22	Simulated nest cavity containing natural grass and fiber nest

* Pregnant female.
** Held in laboratory 5–7 days before experiment.

vival time appreciably. In terms of survival time these animals, by virtue of the small additional protection provided them, were able to increase their survival equivalent to a rise in the temperature of their immediate surroundings of about 5° C. Animals protected by a slightly greater quantity of nesting material were able to increase their survival equivalent to a rise in temperature of their surroundings of about 10° C. Those mice that were provided with natural grass and fiber nests placed in a simulated nest cavity were apparently able to increase their survival equivalent to a rise in temperature of the environment of about 18° C.

Comparison of survival times and total percentage of initial weight lost by winter animals having nest protection with data for unprotected winter animals at the same temperature (Sealander 1951) shows that winter animals thus protected were able to increase their survival equivalent to a rise in temperature of their immediate surroundings of as much as 25° C. Animals protected by cotton nests having a total thickness of only about one-half inch were apparently able to prolong their survival equivalent to a rise in temperature of their immediate surroundings of about 15° C. With better protection in the form of natural grass and fiber nests placed in a simulated nest cavity they were able to prolong their survival equivalent to a rise in temperature of their immediate surroundings of 35° C. or more.

Johnson (1926) obtained data by means of a thermocouple placed inside a nest of *noveboracensis* showing that the nest temperature in cold weather may be as much as 24° C. higher than that of the surroundings. The temperature of the nest will vary, however, from the center to the outside and the differential existing between its temperature and the environmental temperature will depend upon the severity of the air temperature. A thermocouple placed at the exact center of the nest may thus register temperatures which are close to the skin temperature of the mouse, while if it is placed somewhat further out the difference between nest temperature and external temperature will become correspondingly smaller. In the experiments here reported, the thermocouple was placed at a point approximately midway between the center of the nest and its outer surface. Nest temperatures thus recorded ranged from 7–21° C. higher than air temperatures (− 30° to − 35° C.) with a tendency for the gradient to diminish gradually as thermogenetic fatigue of the mouse set in. A rapid decline in nest temperature to that of air temperature marked the point at which the mouse finally succumbed.

Considering that the average monthly minimum temperatures for the central district of Illinois during the coldest months of the year average − 23.9° C. (Mosier 1918), it is improbable that deer mice in this region would be subject to critically low nest temperatures unless situated in very exposed situations. The average minimum for soil at a depth of three inches is − 6.6° C. and it seems improbable that nest temperatures would reach critical levels (around − 15° to − 25° C.) under ordinary conditions unless the food stores of the mouse were exhausted.

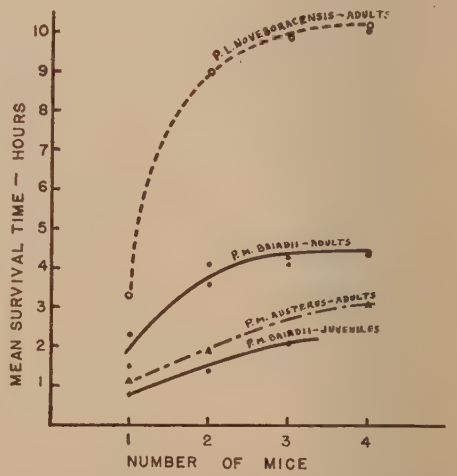

FIG. 1. Effect of huddling on survival time of deer mice without food or water at − 23° C. Cannibalization occurs in all groups of *noveboracensis* and in one group of four *bairdii*.

TABLE II. *The survival time of* Peromyscus *measured singly compared with the mean survival time of two, three, and four mice huddled together at a mean temperature of −23° C.*

Species		Survival time (hours)			
		Number of mice			
		1	2	3	4
Peromyscus m. bairdii	Adults	2.3	4.1	4.3	10.1*
	Adults	1.5	3.6	4.1	4.4
	Juveniles	0.8	1.4	2.1	—
Peromyscus m. austerus	Adults	1.1	1.9	—	3.1
Peromyscus l. noveboracensis	Adults	3.3	9.0*	9.9*	10.2*

* Some cannibalization before removal of carcass.

SURVIVAL IN RELATION TO HUDDLING

The effect of huddling on survival time is shown in Table II and Figure 1. The mean survival time of each individual in the huddle when two mice were huddling together was approximately double that of individuals when exposed singly. Small increases in the mean survival time resulted from increases in the number of individual mice in the huddle, up to three and four, with an evident tendency for the mean survival time of mice huddling in groups of three and four to increase only very slightly over that of huddles of two mice. In a few cases, notably for *noveboracensis* in groups of two or more individuals and in one determination involving a group of four *bairdii,* it was not possible to prevent a small amount of cannibalization of the mice which were the first to succumb by the remaining mice in the huddle even though inspections were frequent. The *noveboracensis,* which showed the most cannibalistic tendencies, were inspected at about ten minute intervals, while the *bairdii,* which seemed to be less cannibalistic, were observed at longer intervals which were, however, progressively decreased throughout the period of observation. Two determinations involving groups of five individuals of each of the above species were discarded for this reason. In the other determinations presented in Table II the amount of cannibalization was very small but evidently greatly prolonged the survival time over that of groups which did not cannibalize.

On theoretical grounds, the increase in survival time as the result of huddling might be expected because of a reduced surface area for heat transfer in relation to the total body mass. In terms of survival time, the most marked difference due to a lowering of the rate of heat loss would

TABLE III. *Weight losses at death by* Peromyscus *measured singly compared with mean weight losses per individual at death by two, three, and four mice huddled together at a mean air temperature of −23° C.*

Species		Total per cent of initial weight lost at death per individual				Per cent of initial weight lost per hour			
		Number of mice				Number of mice			
		1	2	3	4	1	2	3	4
P. m. bairdii	Adults	5.48	8.21	6.98	13.49*	2.37	1.99	1.62	1.33*
	Adults	3.14	4.74	6.42	5.41	2.09	1.32	1.56	1.23
	Juveniles	20.20	7.77	1.98	—	25.23	5.56	0.95	—
P. m. austerus	Adults	3.08	2.01	—	1.41	2.78	1.06	—	0.45
P. l. noveboracensis	Adults	5.51	22.06*	20.94*	23.50*	1.65	2.44*	2.12*	2.31*

* Some cannibalization before removal of carcass.

be expected between two mice huddling together, as opposed to a single individual, with further increases in survival time becoming less in proportion to the progressively smaller reductions in the surface area: body weight ratio. The survival curve would therefore tend to flatten out and reach an asymptote very quickly, some indication of which is shown in Figure 1.

All of the mice with the exception of the *noveboracensis* underwent a reduction in rate of utilization of energy reserves as a consequence of huddling as shown by decreased rates of weight loss per hour with additions to the huddle (Table III). Cannibalization by *noveboracensis* evidently accounted for their much greater survival time. By prolonging their survival time in this way they were apparently able to utilize a much greater percentage of their available energy reserves as shown by the marked increase in total per cent of initial weight lost at death as compared with the other species. The fact that one group of four *bairdii* had a mean survival time almost identical to that of a group of four *noveboracensis,* apparently as a result of cannibalization (Table II), together with a marked increase in the per cent of weight lost at death is additional support for the view that the *noveboracensis* were probably not any more resistant to low temperature.

The per cent of initial weight lost by adult *austerus* and juvenile *bairdii* became less with each addition to the huddle. These animals probably died from a breakdown of temperature regulation before all of their surplus weight could be utilized, even though survival time was considerably prolonged by a reduced rate of weight loss. Adult *noveboracensis* and *bairdii* apparently were able to utilize a greater percentage of their surplus energy in groups of two or more individuals.

No evidence was obtained to account for the marked decrease in survival time of juvenile as compared to adult *bairdii* although it is probable that the juvenile pelage which lacked the longer guard hairs and over hairs offered a less perfect insulation and contributed to a more rapid breakdown of temperature regulation. It is also very possible that the juvenile mice, which were between four and five weeks of age when used, had smaller energy reserves in the form of body fat deposits. It does not seem likely that imperfect temperature regulation from the start was responsible for the shorter survivals of juvenile mice. Although there are no data in the literature pertaining to the development of temperature regulation in *bairdii,* the writer, using thermocouples and an indicator potentiometer to measure skin temperatures, found that in one litter of four *noveboracensis* maximum skin temperatures of between 33.8° and 35.4° C. were reached at 14–15 days of age and were maintained at that level thereafter. More data are available concerning the white mouse and it would seem reasonable that the development of temperature regulation in this rodent is similar to that in wild mice. According to Pembrey (1895) heat regulation is well developed in the white mouse by the tenth day after birth and this is concurred in by Ginglinger and Kayser (1929a, 1929b), Pincus, Sterne, and Enzmann (1933), and Sumner (1913). Sumner, however, states that at temperatures lower than 20–25° C. perfect temperature regulation is not developed until about 20 days of age and depends in part upon the weight of the young animal, heavier individuals having a higher degree of regulation.

Discussion

The tendency of some of the smaller mammals to huddle together in groups at low temperature is a matter of common observation but has been rather generally neglected, with the exception of a few workers (*cf.* Pearse and Hall 1928; Brody 1945), in discussions of body temperature regulation. Thomsen (1945) has reported huddling behavior for *P. l. noveboracensis* and this type of behavior, especially at low temperatures, appears to be characteristic of all members of this genus. Other species of rodents, including the laboratory

mouse and the white rat, and many species of bats exhibit such group responses to low temperature, but among the small insectivores, such as shrews and moles, no gregarious behavior has been reported. The huddling phenomenon is also well marked in some species of birds, *e.g.*, quail and grouse, but is apparently not a characteristic type of behavior among many other species.

Huddling among mice appears to be a purely social behavior pattern which is enhanced by low temperature when it may become of considerable value in group temperature regulation by reducing metabolism through a reduction in the total amount of surface exposed for heat loss. Benedict (1938), from observations on rats, small birds, and on sheep, believes that huddling has no significant influence on metabolism either through reduction of muscular activity or of surface area, but contrary evidence is offered by Brody (1945) and Pearson (1947). The huddling response is probably of definite survival value during prolonged periods of cold under natural conditions when it becomes necessary for the animal to conserve body heat. Gerstell (1942) found that quail which were allowed to huddle together in coveys were able to withstand lower environmental temperatures and for longer periods of time than individual birds, and the ability to resist both low temperatures and nutritive shortages was dependent largely on covey size. Thus at low temperatures a behavior pattern of this sort may become an important aid in conserving heat loss and regulating the body economy.

Mice when huddling at low temperature tend to form a pile. Individuals at the bottom of the pile would be subjected to a temperature considerably above that of the air and would thus be able to avoid hypothermia resulting from too rapid cooling of the blood at the surface. A continual shifting of positions in the huddle would enable each animal to become periodically rewarmed in this way and thus permit it to delay the onset of hypothermia while at the same time enabling it to utilize more of its energy reserves.

Behavior responses of mammals to low temperature have the common function of conserving body heat by increasing the insulative efficiency of the pelage through erection of the fur and by exposing a minimum surface area for conduction, convection, and radiation of heat to the environment. Increased heat production may also be achieved by increased activity at moderately low air temperatures and by involuntary muscular shivering at very low air temperatures. However, in this connection, Giaja (1932) found that rats exercising in the cold exhausted their energies faster, after which they underwent a lowering of body temperature and produced less heat than rats which had rested all the time at the same temperature.

It has been demonstrated experimentally (Hatfield 1940; Wolf 1930) that when the external temperature is lowered to around 0° C., mice exhibit a marked reduction in activity. Hatfield (1938) also found with *Peromyscus m. gracilis* that there was less activity on cold than on warm nights. Due to this curtailment in the animal's activities during periods of cold, it would appear that the protection offered by the nest is of primary importance in tiding it over short periods of extreme cold while that of food consumption may be secondary. It has been observed by a number of writers (Hamilton 1939, 1941, 1943; Burt 1940, 1946; Cory 1912; and others) that *noveboracensis* accumulates stores of food during autumn to carry it through the winter months, but none of these authors gave accurate measurements of the amount of food comprised in the cache or the quantity of utilizable food in the cache. These food stores may be exhausted by the mouse before the termination of cold weather.

It has been shown that both nest protection and huddling increase the survival time of deer mice subjected to low temperatures without food or water. If adequate food stores are not available or are

inaccessible due to coverings of snow or ice during periods of extended cold, such behavior adjustments may be absolutely essential for ensuring survival. The capture of several *noveboracensis* by the writer, after periods of severe weather in mid-winter, which had stub tails of varying lengths in some cases and a dry necrotic condition of the tail in others, indicates that at least a portion of the winter population may have inadequate protection from cold in the form of nests, burrows, or other hiding places. None of the summer *noveboracensis* showed this condition, and this would seem to rule out accidental injury as the cause.

At times when food becomes scarce or difficult of access it becomes necessary for a mouse to range over a much larger area to feed, resulting in a greater expenditure of energy reserves. Periods of extreme cold coupled with a scarcity of food might then become critical by forcing the mouse to expend more of its energy reserves in search of food while at the same time burning up its stored reserves more rapidly in order to maintain a normal body temperature.

The gregarious behavior of deer mice under natural conditions during winter (Cory 1912:187; Hamilton 1943:282; Burt 1946:205; Howard, 1949:15) is probably of definite survival value during cold weather but in the absence of food may possibly lead to increased mortality rates through intraspecific strife. Such self-limiting population mechanisms are known for the muskrat and other mammals (Errington 1946). The cannibalistic behavior shown by deer mice in this study when deprived of food and water at low temperature suggests that such behavior may also occur under natural conditions even though field studies have not as yet demonstrated that it is a factor in winter mortality of deer mice.

Summary

The physiological toleration of extremely low temperatures by mammals may be aided by behavior patterns such as nest-building and huddling. These patterns when superimposed upon normal physiological mechanisms for tolerating heat and cold may permit the animal to live comfortably over a much wider range of temperature than would otherwise be possible.

In this study it was found that both nest protection and huddling prolonged the survival time of deer mice subjected to low temperatures in the absence of food and water.

The nest-building response was better developed in winter *P. l. noveboracensis* than in summer *P. l. noveboracensis,* and the winter animals provided with the same sort of nesting materials were far more resistant to low temperature.

Natural grass and fiber nests placed in a simulated nest cavity provided better protection than exposed nests made of cotton or the simulated nest cavity containing sawdust alone.

Huddling behavior was found to be well developed in individuals of *P. l. noveboracensis, P. m. bairdii,* and *P. m. austerus* and was responsible for prolongation of the survival time of groups of these mice exposed to a mean temperature of − 23° C. without food or water as compared to mice exposed singly. Some cannibalization occurred among *noveboracensis* and *bairdii* exposed to low temperature but did not obscure the effect of huddling upon the survival time.

It is believed that behavior adjustments such as nest-building and huddling constitute thermoregulatory activities which are enhanced at low temperatures and reduced at high temperatures and may be responsible for increased toleration of low temperatures during winter.

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RELICT TRUE PRAIRIE COMMUNITIES IN CENTRAL COLORADO

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The grassland communities of the plains region of Colorado have been studied rather extensively during the past fifty years. There are, however, no reports of relict communities of the true prairies on the Colorado plains, either within the mixed prairie association or within the montane forest communities which extend onto the plains.

The climax vegetation of the Colorado plains is the mixed prairie (Whitfield 1933; Weaver and Clements 1938). Grassland communities make up the vegetative cover of the region with the exception of an extension of the montane forest onto the plains near the summit of the divide which separates the South Platte and Arkansas rivers. This extension of the montane forest is locally known as the Black Forest. During the early phase of an investigation of the Black Forest and adjacent mixed prairie grasslands (Livingston 1949), many communities were observed which were dominated by species typical of the true prairie. These communities occurred both within the forest and at lower altitudes in the adjoining mixed prairie grassland northeast of Colorado Springs. Detailed studies were made of these relict communities to analyze their floristic composition and to determine if possible what factors might permit their maintenance in this semi-arid region where the mixed prairie is the climax.

The writer wishes to express his appreciation to Dr. Henry J. Oosting for his advice regarding the investigation. The writer further wishes to express indebtedness to the late Dr. Frederic E. Clements for his advice and assistance during the early phase of the study.

Climate

The climate of the region is similar to other portions of the Great Plains, being characterized by an arid cold season and a warmer period during which most of the annual precipitation occurs.

Precipitation

Precipitation increases directly with increased altitude. The average annual precipitation in the region under consideration varies from about 16 inches at lower altitudinal stations (6,500 feet) to over 20 inches near the summit of the divide (7,600 feet). Approximately 75 per cent of the total annual precipitation occurs during the six-month period from April through September. The region is characterized by a tendency toward drought in June, a feature not typical of certain other portions of the Great Plains (Smith 1940). In this region all stations show two periods of heavy precipitation, the first occurring in April and May, the second during July and August.

Temperature

Within a given region there is marked variation in temperature at different altitudes. Whitfield (1933) found that with an increase of 1,000 feet in altitude the mean annual temperature decreased about 2.5° in the mountains of Colorado. U. S. Weather Bureau records for stations on the western portion of the Platte-Arkansas divide show a similar mean annual decrease of 2.9° for each 1,000 feet increase in altitude.

Weekly maximum and minimum temperature readings were taken at four stations in grassland communities during the period from June 20 to August 29, 1941, and the data obtained are presented graphically in Figure 1. These data show a rather uniform decrease in both maximum and minimum temperatures with increased altitude. There is no evidence that temperatures within the true prairie communities are appreciably different

from those in adjacent mixed prairie communities.

Evaporation

During the growing season the evaporation rate in the Great Plains is generally high. Whitfield (1933) reported an average weekly loss of 326 cc. from spherical white porcelain atmometers during the summer of 1928 on the plains near Colorado Springs.

The evaporation rates were measured in four grassland communities in this region during the period from June 20 to August 29, 1941, using paired spherical white porcelain atmometers. The average weekly atmometer loss recorded at these stations was: mixed prairie at 6,400 feet, 353.3 cc; true prairie at 6,600 feet, 314.9 cc; true prairie at 7,400 feet, 173.2 cc; and mixed prairie at 7,500 feet, 168.6 cc. These data, presented graphically in Figure 2, indicate a rather uniform decrease in the evaporation rate with increased altitude. There is no evidence that the evaporation rate within the true prairie communities is appreciably different from the evaporation rate in the adjacent mixed prairie.

Soil Moisture

The soils underlying the true prairie relicts are rather uniform in texture. All were sandy loams with the exception of soils at marginal portions of some of the relicts occurring in the forest. The soils near the margin of the communities in the forest were often coarse-textured and contained a rather high percentage of gravel.

Weekly soil moisture determinations were made at five stations during the period from June 20 to August 29, 1941. Duplicate samples were taken with an

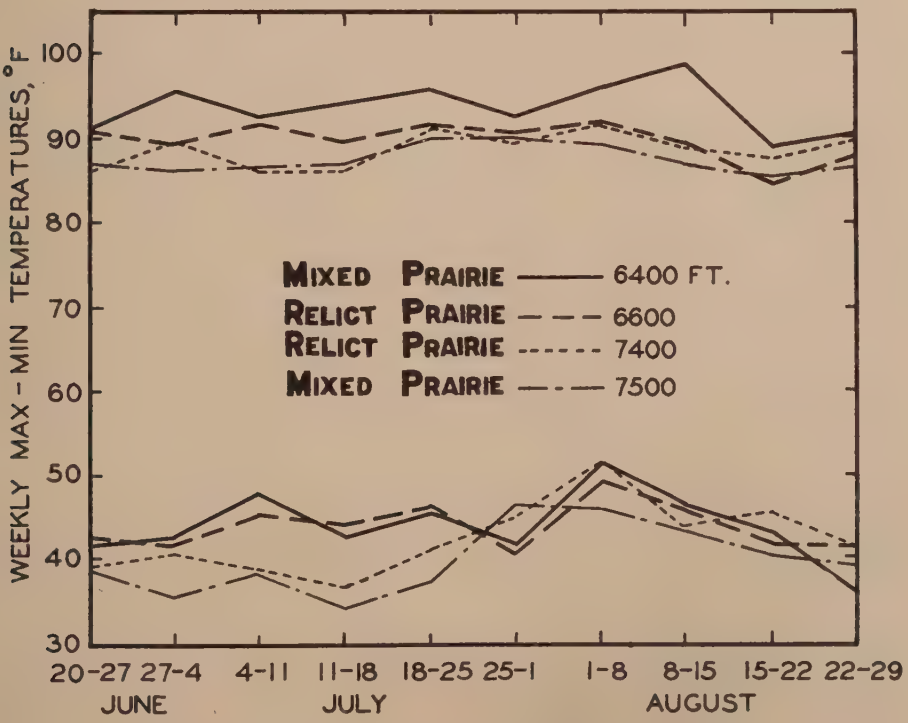

Fig. 1. Weekly maximum and minimum temperatures in mixed prairie and relict true prairie communities for the period from June 20 to Aug. 29, 1941.

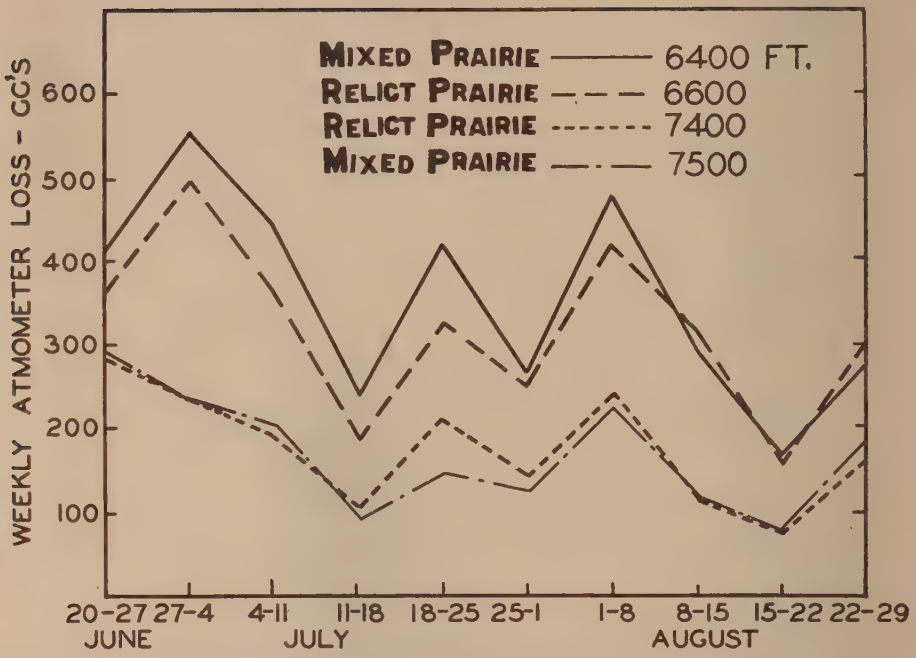

FIG. 2. Weekly evaporation in cubic centimeters in mixed prairie and relict true prairie communities for the period from June 20 to Aug. 29, 1941.

auger at depths of 0 to 1 foot, 1 to 2 feet, and 2 to 3 feet. Soil moisture percentages, determined on an oven dry weight basis, are presented in Table I, together with permanent wilting percentage determinations for samples taken at the same depth levels. Permanent wilting percentages were determined using sunflower plants.

Even during this summer (1941) when rainfall was unusually high in this region, the soil moisture percentage at all depths was occasionally below the wilting percentage in the mixed prairie at lower altitudes. Moisture was always available in true prairie communties, and in the mixed prairie community at 7,500 feet.

Soil moisture data from previous studies in mixed prairie grasslands in this region indicate that the moisture conditions during this period were unusually favorable. Williams and Holch (1945) found soil moisture to be below the hygroscopic coefficient during most of July and August, 1938, in the upper 18 inches of soil in grassland communities near the Black Forest. The present author[1] found soil moisture to be below the wilting percentage for periods of a week or more in surface soils at all altitudes in mixed prairie communities during the summer of 1940.

METHODS

Several methods have proven to be generally satisfactory means of analyzing the vegetation of grassland communities. Two of the commonly used methods were employed in this study.

Line interception method

This method is essentially the same as that described by Canfield (1941). The total ground covered by the basal portion of plants occurring along a line was charted on 1 mm coordinate paper. From this record the percentage of the total

[1] The effect of altitude on the composition of grasslands on the plains of central Colorado. Unpublished thesis, Duke University.

ground covered by all plants was calculated, as was the percentage of the total vegetative cover contributed by individual species. A line fifty meters in length was found to provide an adequate sample of the vegetation at any one site.

Quadrat method

Preliminary analysis of the communities indicated that ten quadrats ½ × 1 meter in size would provide an adequate sample of the vegetation when tested with the species-area curve (Cain 1938). Quadrats were spaced at equal intervals along a straight line, or lines, established in what appeared to be a representative portion of the community. The interval between quadrats, although constant at any one station, varied from 10 meters in small stands within the forest to 25 meters in large stands on the plains.

In each of the quadrats an estimate was made of the total ground area covered by the basal portion of all plants, and of the percentage of this total contributed by each species. All species not important enough to be estimated individually were grouped together; thus the percentages presented in Table II total less than 100 per cent.

Each of the above methods presents advantages which are not characteristic of the other. The line interception method provides a more precise measure of the total cover and of the percentage of the total contributed by each species than does the quadrat method. The quadrat method, however, is advantageous in that it is less time consuming than is the line interception method, especially when the analysis is being made by one man. It appears that the quadrat method provides a reliable qualitative measure of the community, but the quadrat method employed does not give data which were as precise as those obtained by the line interception method.

Vegetation

The climax vegetation characteristic of lower altitudes on the Platte-Arkansas divide is the mixed prairie association; that characteristic of much of the upper portion of the divide is a post-climax ponderosa pine forest. Within both of these major communities occur many relict com-

Table I. *Percentage of moisture in soils at depths of 0–1 foot, 1–2 feet, and 2–3 feet for the period from June 20 to August 29, 1941, and wilting percentage of soils from corresponding positions*

Station	Depth (ft.)	Date of sampling											Wilting per cent
		June		July				August					
		20	27	4	11	18	25	1	8	15	22	29	
Mixed prairie	0–1	3.1	2.0	4.3	2.2	1.9	1.6	6.3	3.5	3.9	8.8	5.9	4.42
6,600 feet	1–2	4.1	2.2	2.5	2.7	1.8	1.6	2.2	4.0	3.0	8.6	6.0	2.14
	2–3	2.0	2.1	3.3	2.3	1.8	1.6	1.6	3.2	2.2	8.7	5.9	2.01
True prairie	0–1	19.3	10.6	9.3	6.6	10.7	6.6	9.4	7.8	14.6	13.0	13.6	6.50
6,600 feet	1–2	20.3	16.1	16.5	9.9	11.9	7.7	7.1	6.3	6.4	11.5	13.4	5.48
Sta. 6	2–3	26.1	14.9	17.5	17.0	19.1	13.6	11.6	9.7	12.2	16.4	19.3	4.76
True prairie	0–1		10.4	17.8	14.3	17.8	16.1	15.4	13.3				8.12
7,300 feet	1–2		11.1	10.9	7.7	12.4	12.0	12.8	13.3				9.31
Sta. 2	2–3		12.2	18.5	10.8	14.2	13.0	12.2	13.3				10.05
True prairie	0–1		10.9	19.4	11.4	13.5	12.2	15.8	7.4	23.6	27.3	23.1	7.66
7,400 feet	1–2		10.1	17.1	17.4	18.8	15.8	12.5	10.1	14.4	31.1	25.0	6.57
Sta. 4	2–3		12.5	14.9	11.9	16.5	14.0	12.0	13.8	12.2	26.6	26.8	8.80
Mixed prairie	0–1	40.0	12.7	19.4	16.0	19.6	16.4	23.3	18.1	20.5	26.4	22.7	6.25
7,500 feet	1–2	29.5	16.8	15.7	13.6	18.4	14.9	19.8	17.9	17.4	17.5	20.9	9.57
	2–3	29.1	14.4	16.2	16.6	16.2	15.4	18.3	17.9	18.0	17.6	20.1	8.65

munities of true prairie vegetation. The relicts within and immediately adjacent to the forest had among their important dominants *Sporobolus heterolepis,*[2] *Stipa spartea* and *Poa pratensis.* Dominants of the relict communities occurring at lower altitudes in the mixed prairie include *Sporobolus heterolepis, Andropogon scoparius* and *Sorghastrum nutans.*

Relict communities within the forest

The relict areas occurring in the forest vary in size from a few clumps of plants at a given site to areas several acres in extent. These relicts occur generally in valleys and swales throughout the forest. They are best developed near the heads of these valleys, but are also present as marginal zones along the meadows which occupy the lower portion of the valleys.

[2] Hitchcock's *Manual of the Grasses of the United States,* U. S. Dept. Agr. Misc. Pub. No. 200 (1935) was used in the identification of all grasses. Smith and Durrell's *Sedges and Rushes of Colorado,* Colo. Agr. Expt. Sta. Tech. Bull. 32 (1944) was used in the identification of these groups, and Coulter and Nelson's *New Manual of Botany of the Central Rocky Mountains,* American Book Co., New York (1909) was used in the identification of all other plants.

TABLE II. *Floristic composition of relict communities showing frequency percentage (f) and percentage of ground cover*

	Stations in Black Forest Region						Stations in Plains Region						
	1		2	3	4		5		6		7		
											Up	Mid	Low
Total basal cover	20.5		16.5	17.1	23.5		21.5		19.8		19.5	18.8	18.7
A. Dominant Grasses	f	Per cent basal cover	Per cent basal cover	Per cent basal cover	f	Per cent basal cover	f	Per cent basal cover	f	Per cent basal cover	Per cent basal cover	Per cent basal cover	Per cent basal cover
Agropyron pauciflorum	10	tr			10	0.1			50	8.0	tr		
Andropogon furcatus	10	5.2			10	0.4	70	6.5	30	5.2			
Andropogon scoparius	10	2.1	2.3	3.7			95	26.2	90	25.3	47.2	28.7	55,8
Bouteloua gracilis			14.2	6.8			100	19.3	30	1.1	31.0	4.9	15.0
Danthonia spicata	20	4.9	5.6	9.3	20	0.4	40	3.1				4.6	
Koeleria cristata	10	0.1	2.8	1.3	50	0.4	30	2.8	10	2.0	3.2	2.9	1.8
Muhlenbergia montana	80	4.9	5.6	9.3	20	0.4	40	3.1				4.6	
Poa compressa			10.5	2.3	20	1.3							
Poa pratensis	80	31.4	6.6	6.4	40	4.6						0.3	
Sorghastrum nutans							10	4.1	30	7.6	0.3	30.7	2.1
Spartina pectinata									50	4.1			
Sporobolus heterolepis	70	29.1	10.1	33.9	100	73.4	40	12.5	100	30.7	2.9	9.5	1.5
Stipa spartea	40	7.0	2.9	5.4	10	tr							
Totals		88.9	59.3	72.0		80.6		74.5		84.0	84.6	81.6	76.2
B. Subdominant Grasses, Sedges and Rushes (In Forest and on Plains)													
Agropyron smithii				0.4	10	tr	10	0.4			0.5	0.2	
Agropyron subsecundum	20	tr	0.8	0.8	20	0.5			10	tr			
Agrostis alba					20	0.5			50	4.1			
Agrostis hiemalis	20	0.1	tr	0.4	10	tr	10	0.4	10	1.0			
Carex heliophila	60	2.9	3.7	0.8	10	tr	10	0.3					
Carex oreocharis			tr	1.8			10	0.2			tr	0.2	0.7
Eleocharis palustris					10	tr			10	tr			
Juncus balticus					90	2.0	60	0.8	40	0.8	tr	0.1	1.2
Muhlenbergia squarrosa			tr		10	0.5			20	1.8		1.8	
Phleum pratense			2.0	0.4					30	0.3			
(In Forest Only)													

TABLE II—*Continued*

	Stations in Black Forest Region						Stations in Plains Region						
	1		2	3	4		5		6		7		
											Up	Mid	Low
Total basal cover	20.5		16.5	17.1	23.5		21.5		19.8		19.5	18.8	18.7
B. Subdominant Grasses, Sedges and Rushes (In Forest and on Plains)	f	Per cent basal cover	Per cent basal cover	Per cent basal cover	f	Per cent basal cover	f	Per cent basal cover	f	Per cent basal cover	Per cent basal cover	Per cent basal cover	Per cent basal cover
Blepharoneuron tricholepis		10	tr	2.5	3.7								
Bromus inermis				0.4									
Calamogrostis inexpansa						10	tr						
Carex brevior						20	5.3						
Carex lanuginosa						20	1.3						
Elymus canadensis			0.5										
Festuca octoflora			0.7										
Muhlenbergia wrightii				2.3									
Sitanion hystrix	40	0.1	0.7										
Stipa columbiana			0.7										
Stipa viridula			tr	tr									
(In Plains Only)													
Andropogon hallii													0.9
Calamovilfa longifolia							90	8.1	30	0.9	10.6		0.8
Carex aurea									10	tr			
Carex filifolia											tr		1.5
Carex nebraskensis									10	tr			
Carex praegracilis									10	tr			
Hordeum jubatum												tr	
Juncus longistylis									20	0.2	0.4	0.1	
Juncus Torreyi									20	tr	0.1		
Muhlenbergia asperifolia									10	tr			
Panicum virgatum							10	1.3	30	1.6	0.9	0.3	0.5
Poa fendleriana									10	0.4			
Sporobolus cryptandrus													0.2
Stipa comata													0.9
Totals		3.1	12.0	10.6		10.1		11.5		11.1	12.5	2.7	6.7
C. Forbs (In Forest and on Plains)													
Achillea millefolium	40	tr	tr		70	0.7			20	0.2		tr	
Allium cernuum			tr	tr	20	tr	40	1.2	10	0.2			
Antennaria aprica	10	tr	5.0		10	tr	10	0.5	40	1.8		6.1	tr
Artemisia campestris			tr				25	1.2					tr
Artemisia frigida	40	tr		tr			30	0.3					4.5
Artemisia gnaphalodes			tr	tr	10	tr			10	tr			
Aster multiflorus	30	tr			70	0.2	15	0.9	40	1.1	tr	tr	tr
Chenopodium leptophyllum	10	tr									tr		tr
Chrysopsis villosa	10	0.3	0.6				10	tr					
Euphorbia glyptosperma			tr	tr									tr
Helianthus rigidus			tr	tr					20	0.4			
Liatris ligulistylis			tr	tr					10	0.5			
Liatris punctata	10	tr		tr								tr	
Orthocarpus luteus	10	tr	tr	tr			25	tr	10	tr			
Pentstemon angustifolius				tr								tr	
Plantago Purshii			tr				10	tr					
Polygonum exertum			tr				5	tr					
Solidago missouriensis	10	0.1	1.9	1.4			35	2.3	10	0.2	tr	3.3	8.2
Solidago nemoralis	40	0.8					45	3.5	30	1.3	2.6		
Solidago rigida			1.7	1.8	50	1.1	10	tr	30	0.7		2.0	2.3
Thermopsis montana			tr	tr	70	1.2	10	tr					

TABLE II—*Continued*

	Stations in Black Forest Region						Stations in Plains Region						
	1		2	3	4		5		6		7		
											Up	Mid	Low
Total basal cover	20.5		16.5	17.1	23.5		21.5		19.8		19.5	18.8	18.7
C. Forbs (In Forest and on Plains)	f	Per cent basal cover	Per cent basal cover	Per cent basal cover	f	Per cent basal cover	f	Per cent basal cover	f	Per cent basal cover	Per cent basal cover	Per cent basal cover	Per cent basal cover
Trifolium pratense	10	0.1							10	0.2			
Veronica peregrina			tr	tr			5	tr					tr
Vicia americana				tr	10	0.1			10	0.2			
(In Forest Only)													
Anogra coronopifolia				tr									
Aragallus Lambertii				tr									
Arenaria Fendleri	10	tr											
Arnica cordifolia			1.2										
Artemisia dracunculoides	30	0.3		0.6									
Aster laevis				tr									
Aster Porteri			7.6	tr									
Astragallus bisulcatus				tr									
Calochortus Gunnisonii			tr										
Campanula rotundifolia	30	tr		tr									
Chenopodium album			tr										
Drymocallis arguta	10	0.1	tr	tr									
Drymocallis fissa	10	tr											
Erigeron asper	30	0.8	tr	0.7	10	tr							
Erigeron flagellaris	10	tr	1.7	3.8									
Erigeron radicatus				1.1									
Galium boreale				0.8	20	0.2							
Gayophytum ramosissimum			tr										
Geranium Parryi	10	tr		tr									
Gnaphalium decurrens	10	tr											
Heuchera parviflora	20	tr											
Iris missouriensis				tr	10	0.2							
Krigia virginica	10	tr											
Lithospermum angustifolium				tr									
Lychnis Drummondii	20	tr											
Mertensia lanceolata	50	tr		tr	10	tr							
Monarda menthaefolia	10	tr	tr										
Oxalis stricta	10	tr											
Pedicularis canadensis					10	tr							
Pentstemon glaber				1.5									
Pentstemon humilis			tr	tr									
Potentilla effusa	10	tr			50	2.8							
Potentilla gracilis			tr	0.9									
Polygonum aviculare				tr									
Polystichium sp.			4.7										
Pulsatilla hirsutissima	20	tr	1.1	tr									
Rosa arkansana	80	1.6	tr	tr	20	tr							
Scutellaria Britonii	20	tr		tr									
Sedum stenopetalum			tr										
Smilacina stellata	20	0.3											
Taraxacum officinalis			tr										
Tragopogon porrifolius	20	tr											
Troximon glauca	10	0.3		tr	20	0.2							
(In Plains Only)													
Ambrosia artemisifolia											tr	tr	
Anogra strigosa							10	tr					
Aster Geyeri									40	0.5			

TABLE II—*Continued*

	Stations in Black Forest Region						Stations in Plains Region						
	1		2	3	4		5		6		7		
											Up	Mid	Low
Total basal cover	20.5		16.5	17.1	23.5		21.5		19.8		19.5	18.8	18.7
C. Forbs (In Forest and on Plains)	f	Per cent basal cover	Per cent basal cover	Per cent basal cover	f	Per cent basal cover	f	Per cent basal cover	f	Per cent basal cover	Per cent basal cover	Per cent basal cover	Per cent basal cover
Aster Ptarmacoides							5	tr	40	0.2			
Commandra pallida									10	tr			
Equisetum arvense												tr	tr
Erigeron sp.									10	tr			
Eriogonum annuum							5	tr					
Gentiana affinis							15	tr					
Gentiana strictiflorus									10	tr			
Gilia aggregata												tr	tr
Glycyrrhiza lepidota									30	1.1			
Hedeoma hispida							40	0.1			tr		
Helenium autumnale									10	tr			
Lappula occidentalis							15	tr					
Leptilon canadensis							5	tr					
Lobelia syphilitica									10	0.4			
Melilotus alba									10	0.4			
Petalostemon purpureus							85	1.4	50	1.4	0.2	tr	0.9
Prunella vulgaris									30	tr			
Rudbeckia hirta									10	tr			
Salsola pestifer							10	tr					
Senecia mutabilis									10	tr			
Silene Scouleri													tr
Sisyrinchium angustifolium							5	tr	20	tr			
Talinum parviflorum							15	1.2					tr
Thelasperma gracile							5	tr					
Trifolium repens							5	tr	20	tr			
Triglochin maritima									10	tr			
Viola adunca									20	0.5			
Opuntia polyacantha											0.1		
Total Cover, Forbs		4.7	25.5	12.6		6.7		12.6		11.3	0.3	14.0	15.9

Representative communities were observed throughout the forest and quantitative studies made at four stations at altitudes between 7,200 feet and 7,500 feet. These communities were usually not over 50 meters in width, were frequently savannah-like, and most were shaded during a part of the day by pines which were either within or at the borders of the community (Fig. 3). Station 4, supporting an almost pure stand of *Sporobolus heterolepis,* occupied a site differing topographically from the usual. It occurred near the head of a flat, open valley, was more than 100 meters in width, and no part of the community was shaded by pines.

Of the grasses reported by Weaver and Fitzpatrick (1934) as the most important in the true prairie, only a few were not found in these communities. Those not recorded were *Panicum virgatum, Sorghastrum nutans, Spartina pectinata,* and *Bouteloua curtipendula.* A complete list of all species recorded at these stations is presented in Table II.

The communities studied in the forest varied rather widely in their composition and structure. They appeared to be expressions of the true prairie, but were altered in varying degrees by the presence of mixed prairie and montane species. From field observations it appeared that

FIG. 3. Typical relict true prairie community at margin of meadow in the Black Forest at station 1.

the importance of the mixed prairie species was correlated with a lower soil moisture content, whereas montane species were most important near the margins of the communities, especially in the shade of pines. All communities were characterized by the dominance of either or both *Sporobolus heterolepis* and *Stipa spartea* in combination with *Poa pratensis, Danthonia spicata,* and *Muhlenbergia montana.* Species common to all stations, and of importance in one or more, were *Sporobolus heterolepis, Stipa spartea, Poa pratensis, Muhlenbergia montana, Koeleria cristata,* and *Carex heliophila.*

Station 1 was located at an altitude of 7,500 feet in the west central part of the forest. Dominants of the community were *Poa pratensis, Sporobolus heterolepis, Danthonia spicata,* and *Stipa spartea,* and made up 31.4, 29.1, 9.1 and 7.0 per cent of the total cover respectively. Several associated grasses were more important than were any of the forbs and included *Andropogon furcatus, Muhlenbergia montana* and *Andropogon scoparius.* The most important forbs were *Solidago nemoralis* and *Erigeron asper,* each making up 0.8 per cent of the total cover.

Station 2 was located near the north central border of the forest at an altitude of 7,300 feet. The area was the only one included in the study which had been grazed at all heavily. Although several true prairie species were present, they were of less importance than at any other station. The dominants were *Bouteloua gracilis, Poa compressa* and *Sporobolus heterolepis* and contributed 14.2, 10.5, and 10.1 per cent of the total cover respectively.

The abundance of Bouteloua was probably the result of heavy grazing since it was of secondary importance in all other relicts studied. *Poa compressa* was also of greater importance in this community than at any other, being especially important in areas where the soil was thin.

As elsewhere the grasses were the most

important associated species. Those of greatest importance were *Poa pratensis, Muhlenbergia montana, Danthonia spicata, Koeleria cristata, Stipa spartea, Blepharoneuron tricholepis* and *Andropogon scoparius.* Other important species included *Cares heliophila, Aster porteri* and *Antennaria aprica.*

Station 3, located near the south central border of the forest at an altitude of 7,200 feet, supported a savannah-like growth. The most important species in the community was *Sporobolus heterolepis* which made up 33.9 per cent of the total cover. Other grasses in addition to the dominant which approached dominant importance contributed only 9.3 to 5.4 per cent of the total cover. They were *Muhlenbergia montana, Bouteloua gracilis, Poa pratensis* and *Stipa spartea.* Important grasses other than these were *Blepharoneuron tricholepis, Danthonia spicata, Poa compressa* and the sedge *Carex oreocharis.* Of the important associated species only three were forbs. These were *Erigeron flagellaris, Solidago rigida* and *Pentstemon glaber.*

Station 4 was located in a broad flat valley near the center of the forest at an altitude of about 7,400 feet. *Sporobolus heterolepis* dominated this community and made up 73.4 per cent of the cover. Associated species of importance were *Carex heliophila, Poa pratensis, Juncus balticus* and *Potentilla effusa.* Of these, only *Juncus balticus* was of general importance throughout the stand. The others were of local importance in different parts of the area.

Studies of zonation across several open meadows which were bordered by true prairie relicts indicated the following general zones of vegetation. Near the outer edge of the meadow, varying from one to five meters in width, was a true prairie zone dominated by *Stipa spartea.* Associated with and frequently codominant with Stipa were one or more of the following species: *Muhlenbergia montana, Andropogon scoparius,* and *Danthonia spicata.* Other species included *Koeleria cristata, Juncus balticus, Rosa arkansana* and *Artemisia campestris caudata.*

The next zone, also true prairie, varied from a few meters to more than twenty meters in width, and was dominated by *Sporobolus heterolepis.* Species frequently associated with and sometimes codominant with Sporobolus were *Poa pratensis,* and *Stipa spartea.* Additional species generally present in the zone were *Koeleria cristata, Agropyron subecundum, Poa compressa, Erigeron flagellaris, Astragalus bisulcatus, Krigia virginicus, Juncus longistylis, Oxalis stricta, Solidago missouriensis* and *Allium cernuum.*

The next zone was usually rather narrow, but at times as much as ten meters in width. It was usually dominated by *Agrostis alba* and *Eleocharis palustris.* At times *Agrostis hiemalis, Phleum pratense* and *Poa pratensis* were important, becoming codominant with the above species. Important associated species other than these were *Muhlenbergia squarrosa, Trifolium pratense, Juncus tenius, Juncus longistylis* and *Carex interior.*

A hydric community occupied the wet bottom of the meadow and was dominated almost exclusively by *Carex nebraskensis.* The most important associated species were *Juncus torreyi* and *Eleocharis palustris.*

The dominants of these last two zones have a rather wide distribution, and are not nesessarily typical of the true prairie.

Relict communities within the mixed prairie

Extensive relict communities of true prairie vegetation are common in certain localities southeast of the Black Forest at altitudes as low as 6,500 feet. The Black Squirrel Creek drainage area in the vicinity of Falcon and Peyton is especially rich in these relicts, and there is evidence to indicate that overgrazing may have destroyed extensive former relicts in this locality. Many of these relict communities appear to have been maintained by the landowners in essentially their original

condition, since the lands have proven to be more valuable for the production of hay than for year-around grazing. Hence, grazing is usually restricted to the fall and winter months following mowing in late summer. Such management was practiced on all areas included in this portion of the study.

These communities occur typically on lands where the water table is near the surface in a region where springs are common. Soils are sandy loams in which moisture is available during the entire growing season.

Topographically the area is characterized by rolling prairies and flat plains. It is on the flat plains and along streams that the communities attain their best development. The presence of other species with *Sporobolus heterolepis,* and the complete absence of *Stipa spartea* and *Danthonia spicata* make the general aspect of the communities quite unlike the relicts within the forest.

Three large relicts were studied in the Falcon-Peyton locality. Two areas (stations 5 and 6) were on relatively flat plains and were relatively uniform in composition. The other area (station 7) bordered a small stream and exhibited well defined zonation.

The dominants at station 5 were *Andropogon scoparius, Bouteloua gracilis* and *Sporobolus heterolepis.* These species made up 58 per cent of the total cover (Table II) : Andropogon contributing 26.2 per cent, Bouteloua 19.3 per cent and Sporobolus 12.5 per cent. The abundance of some of the true prairie species is shown in Figure 4.

The abundance of *Bouteloua gracilis* was apparently caused by previous overgrazing, for the owner reported that this range had been overgrazed until a few

Fig. 4. The relict true prairie community at station 5.

years previously when grazing during the spring and early summer months was discontinued.

The most important associated species were all grasses, and included *Calamovilfa longifolia, Andropogon furcatus, Sorghastrum nutans* and *Koeleria cristata.* Most important of the forbs were *Solidago nemoralis* and *Petalostemon purpureus.*

The best preserved relict observed in the locality (station 6) contained many species not recorded at other stations. Among the plants recorded here, but not in other stands on the plains where detailed studies were made, were *Spartina pectinata, Lobelia siphilitica, Viola adunca, Helenium autumnale, Glycyrrhiza lepidota, Triglochin maritima, Carex aurea* and *Carex praegracilis.* In addition to these species, all of which were recorded in the quadrats, one species of particular interest was found in moist soil near a spring. This plant was *Juncus brachycephalus* (Engelm) Buch, a species of the northeastern United States. Its westernmost record previously was in Minnesota. This plant may have been an introduction; however, inasmuch as many other eastern species are present in the area, it appears that it may also be a relict species.

The dominants of the community were *Sporobolus heterolepis, Andropogon scoparius, Agropyron pauciflorum* and *Sorghastrum nutans. Sporobolus heterolepis* and *Andropogon scoparius* were of general occurrence throughout the community. *Agropyron pauciflorum* was most abundant on drier areas in association with the two major dominants, while *Sorghastrum nutans* was most abundant in the more moist sites where it was the aspect dominant because of its greater height. The dominants made up over 66 per cent of the total cover; Sporobolus making up 28.0 per cent, Andropogon 24.2 per cent, Sorghastrum 7.9 per cent, and Agropyron 6.5 per cent.

The most important of the associated plants were all grasses, *Andropogon furcatus, Agrostis alba, Spartina pectinata,* and *Koeleria cristata* being of greatest importance. The forbs of greatest importance were *Antennaria aprica, Petalostemon purpureus, Solidago nemoralis, Aster multiflorus* and *Glycyrrhiza lepidota.*

The best defined zonation observed in the entire region was along a small stream east of Falcon at station 7. Hydrophytic and halophytic zones, as well as true prairie and mixed prairie zones, were present. The width of the zones varied with the topography from a few meters to well over 100 meters between the stream and the outer portion of the true prairie where it was replaced by the mixed prairie. The area studied had a width of approximately 100 meters on each side of the stream.

The upland drier areas beyond the outermost true prairie zone was mixed prairie dominated by *Bouteloua gracilis* and *Stipa comata.*

Three well defined zones having true prairie species as their most important constituents formed a broad band below the climax mixed prairie and usually occupied over half the distance between the mixed prairie and the stream. These three zones were about equal in width. The upper and lower zones were very similar in composition, but differed markedly from the central zone as indicated in Table II.

The dominants in both the upper and lower zones were *Andropogon scoparius* and *Bouteloua gracilis.* The most abundant associated species in the upper zone were *Solidago missouriensis, Artemisia frigida* and *Solidago rigida.* Thus, this community was the only stand investigated in which the forbs were of greater importance than were the associated grasses. Grasses of secondary importance were *Sorghastrum nutans, Koeleria cristata* and *Sporobolus heterolepis.* The most important associated species in the lower zone were *Calamovilfa longifolia, Koeleria cristata* and *Sporobolus hetero-*

lepis. Here, forbs were of little importance, and only one, *Petalostemon purpureus,* made up a measurable per cent of the total cover.

The central zone of the three characterized by true prairie species was dominated by *Sorghastrum nutans, Andropogon scoparius* and *Sporobolus heterolepis.* The associated grasses of greatest importance were *Bouteloua gracilis, Muhlenbergia montana* and *Koeleria cristata.* Only four forbs made up a measurable per cent of the total cover. They were: *Antennaria aprica, Solidago missouriensis, Solidago nemoralis* and *Solidago rigida.*

Bordering the lowermost true prairie zone on the downslope side was a halophytic zone characterized by such halophytes as *Distichlis stricta, Sporobolus airoides* and *Salicornia rubra.* The community was dominated by *Bouteloua gracilis, Distichlis stricta* and *Sporobolus airoides.* The only important associated grass was *Agropyron smithii,* although three other grasses were recorded. They were *Festuca octoflora, Bouteloua simplex* and *Calamovilfa longifolia.*

A hydrophytic community occupied a relatively narrow zone near the stream. This zone was rarely over 5 meters in width, and *Carex nebraskensis,* the dominant, made up over 50 per cent of the total cover. Other species of importance included *Juncus balticus, Carex brevior* and *Carex hallii.*

Discussion

Many stands of true prairie vegetation occur within the Black Forest and in the adjacent mixed prairie region at lower altitudes on the Platte-Arkansas divide. These communities are composed largely of species typical of the true prairie, together with associated species from the mixed prairie and montane associations. Many of the species consistently present in these communities do not appear in the mixed prairie of the region, and a few had not been reported in Colorado.

Among the species not generally found in the mixed prairie community, but important in the relict communities, are *Sporobolus heterolepis, Stipa spartea, Poa pratensis, Helianthus rigidus, Solidago rigida,* and *Rosa arkansana.* Two of these, *Sporobolus heterolepis* and *Stipa spartea,* together with *Sporobolus asper* (a species not found in these communities), are the most characteristic dominants of the true prairie and do not occur as dominants in any other association (Weaver and Clements 1938). Many of the species numerically unimportant, such as *Aster laevis, Glycyrrhiza lepidota, Stieronema ciliatum, Rudbeckia hirta, Pedicularis canadensis* and *Oxalis stricta,* further indicate that these communities are expressions of the true prairie.

Many other species which occur occasionally in the mixed prairie as subordinates, occur in these communities as dominants or important associated species. Among these are *Andropogon scoparius, Andropogon furcatus, Sorghastrum nutans, Spartina pectinata, Panicum virgatum, Juncus balticus* and *Petalostemon purpureus.* The one important true prairie species occurring in the mixed prairie communities of this region, but not found in these relicts, is *Bouteloua curtipendula.*

The relict communities within the limits of the Black Forest vary somewhat in composition from those found at lower altitudes on the plains. The most obvious variations are between the dominants in the two localities. *Stipa spartea* and *Danthonia spicata,* often among the dominants in the communities found in the forest, are absent at the plains sites. *Sorghastrum nutans, Andropogon scoparius* and *Agropyron pauciflorum,* among the dominants in the plains communities, are absent or relatively unimportant in the communities found in the forested region.

Relict true prairie communities have been able to survive in this semiarid region only in very mesic sites. Mesic conditions of the relict areas in the forest result principally from their topographic position, but sites on the plains at lower

altitudes are more moist than surrounding areas because of a higher water table.

Neither precipitation, temperature, nor evaporation appears to be the causal factor influencing or limiting the presence of these communities. The increase in rainfall with increased altitude is no greater in the relict areas than in other communities of equal altitude. Similarly, temperatures are not significantly different in true prairie and mixed prairie communities at the same altitude. Evaporation rates within the relict communities in the forest are lower than are evaporation rates in mixed prairie grasslands at higher altitudes, but this is probably not a critical factor since relicts occur at lower altitudes on the plains where the evaporation rate is much higher than that in the mixed prairie communities near the summit of the divide.

Differences in soil texture are not great between the communities found in the forest and those at lower altitudes on the plains; however, variations in soil texture were noted within some of the relicts in the forest. Soils of marginal areas of some of the communities are coarse-textured, and it is on these soils that *Stipa spartea* is most abundant. Since this species generally occurs on coarse-textured soils (Weaver and Fitzpatrick 1934), it would appear that its absence on fine-textured soils at the plains sites is to be expected.

The prime factor permitting the development and maintenance of these relict communities appears to be the increased soil moisture. Soil moisture was available at all sites on each sampling date, yet frequently was not available in adjacent mixed prairie communities.

Causes for the development of the true prairie communities in the forested area near the summit of the divide are not clear. Evaporation rates and temperatures in the forest stands and the included true prairie communities are not significantly different, thus would not appear to be the factors causing the development of the true prairie community in these sites. Likewise soil moisture does not appear to be a causal factor. However, since there is marked variation in the texture of soils in the forest and true prairie communities, it appears probable that this is the factor most important in causing the development of the two communities. The presence of fine-textured soils in the true prairie areas might well retard root development of pine seedlings to such an extent that they would be unable to survive unfavorable periods, particularly in the fall and winter months when precipitation is at a minimum. That this may be true is indicated by the fact that pine seedlings observed during the summer of 1941 in the true prairie community at station 2 had all failed when the area was again observed in 1946.

These relict communities, occurring far west of the normal range of the true prairie, may have been initiated in one of several ways. Clements (1936) states that relicts fall into one of two well defined groups: first, those due to climatic pulsations, and secondly, those produced by human coaction. There is a possibility that these communities may have resulted from either of the above causes.

First, they may have resulted from human coaction. A few of the species occurring in the communities, such as *Poa pratensis* and *Phleum pratense,* are known to have been introduced into the region as lawn or pasture grasses. There is then a possibility that other true prairie species have likewise been introduced and have since become established. However, since these communities are rather widespread, and since they are relatively constant in composition, it seems unlikely that they have resulted from such coaction.

A second possibility is that the communities are natural invasions, having resulted from a westward migration. Inasmuch as the forest community has migrated from the Rocky Mountains eastward into the true prairie region (Pound and Clements 1900) it is possible that the same migration path may have been fol-

lowed westward by the true prairie species, since the forest contains microclimatic areas suitable for their development and maintenance.

A third possibility, and one that seems more probable, is that these true prairie communities are relicts of a former climax. It is generally conceded that the prairies were driven southward and westward before the advance of the glaciers during the Pleistocene epoch. When the glaciers receded the climate became drier and the true prairie retreated to the north and east. During this retreat relicts of the true prairie could have been left behind in the more mesic sites where they have been able to survive.

Summary

1. The climax vegetation characteristic of lower altitudes on the Platte-Arkansas divide is the mixed prairie association; that characteristic of much of the upper portion of the divide is an extension of the montane forest onto the plains. Within both of these communities occur many relict grassland communities dominated by species typical of the true prairie. The relicts within and immediately adjacent to the forest include among their important dominants *Sporobolus heterolepis, Stipa spartea* and *Poa pratensis*. Dominants of the relicts occurring at lower altitudes within the mixed prairie include *Sporobolus heterolepis, Andropogon scoparius* and *Sorghastrum nutans*. Associated with these dominants are numerous subordinate species which are characteristic of the true prairie.

2. Neither precipitation, temperature, nor evaporation appears to be the causal factor influencing or limiting the presence of these communities.

3. These relict true prairie communities have been able to survive in this semi-arid region only in sites where soil moisture conditions are unusually favorable. Increased soil moisture at sites of the relicts is largely influenced by the topographic position of the communities in the forest (at margins of open meadows), and by an unusually high water table at the sites within the mixed prairie.

4. It is possible that these relict communities may have resulted from man's activities, having been recently established from seed introduced from the eastern true prairie region. There is, however, little evidence to support this view. Secondly, they may have originated from a westward migration from the true prairie, following the same migration path that led the Rocky Mountain forest communities eastward into the true prairie region of Nebraska. A third and more probable explanation of the origin of these relict communities, is that they are relicts of a former climax. It is generally conceded that the prairies were driven westward and southward before the advance of the glaciers. When the glaciers receded the climate became drier and the true prairie retreated to the north and east. During this retreat relicts of the true prairie could have been left behind in the more mesic sites where they have been able to survive.

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THE ECOLOGY OF THE MOUNTAIN POCKET GOPHER, *THOMOMYS MONTICOLA*

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There has been very little experimental work done on the ecology of pocket gophers in spite of their great economic importance. Perhaps the most complete account is that of *Thomomys talpoides morrei* in Montana by Tyron (1947) who apparently was one of the first to utilize live trapping as a means of study of these animals. Miller (1946) and Storer (1947) give some pertinent data on *Thomomys bottae* in California valleys. The mountain species, *Thomomys monticola,* received considerable attention as agents of soil and water conservation by Grinnell and Storer (1924), Grinnell (1923, 1933) and by Storer, Evans and Palmer (1944). Ellison (1946) and Ingles (1949a) dealt with soil erosion and water relations, respectively, of the mountain species. The present paper results from a study of this species in two small mountain meadows near Huntington Lake, California, during the spring, summer, and autumn months in the years 1947 through 1950.

The plant identifications were made by Charles Quibell of Fresno State College and Roxana S. Ferris of the Dudley Herbarium, Stanford University. Sheets of the plant specimens were stored in the Dudley Herbarium. The arthropods were identified by various experts connected with the Smithsonian Institution under the direction of Edward A. Chapin, Curator of the Division of Insects. All of the arthropod specimens were given to the Smithsonian Institution.

Environment

Huntington Lake lies at the lower margin of the Red Fir Forest (Munz and Keck 1949) at 2140 meters (7,000 feet) elevation in the Sierra Nevada mountains 112 kilometers (70 miles) east of Fresno, California. One small meadow (College Meadow), 0.8 hectares or two acres in extent, is located near the northeast edge of the lake and is completely surrounded by pure stands of lodgepole pines (*Pinus Murrayana*). In the summer and autumn months it becomes dry and devoid of green leafy herbaceous vegetation. Most of the meadow is flat, poorly drained, and is very wet only in the spring when the snow is melting. These soil and moisture conditions are apparently ideal for the growth of two important food plants of the mountain pocket gopher, the corms of *Tritileia ixioides* var. *analina* and the tuber-like roots of *Lewisia nevadensis*. By the first of June the entire area is covered with an unidentified species of fine grass and with miners' lettuce (*Montia perfoliata*) near the edge of the woods.

The other meadow (Mule Deer Meadow) is about a mile north of the lake and forms the headwaters of Strawberry Creek. It is some 150 meters (500 feet) higher than the lake and is surrounded by a fringe of lodgepole pines with red fir and Jeffrey pines on the surrounding mountain slopes. Only 0.8 of 2.63 hectares (6.5 acres) are dry enough for pocket gopher occupancy. The rest of the meadow is very wet and can be occupied by pocket gophers only while snow covers its surface. Water and snow as ecological factors affecting this species of pocket gopher on this meadow were studied and reported previously (Ingles 1949a).

Many kinds of plants grow on the meadow, which remains green throughout the summer and autumn months. It is usualy grazed by cattle for a period of two to four weeks after the middle of August. On the wettest areas are such hydrophilous plants as: *Trifolium Wormskjoldii, Spiranthes Romanzoffiana, Gentiana simplex, Veronica serphyllifolia, Carex rostrata,* and unidentified species of

mosses. On areas dry enough to support pocket gophers all of the year are such plants as: *Stipa Lettermanii, Poa pratensis, Agrostis idahoensis, Juncus orthophyllus, Rumex salicifolius* var. *denticulatus, Achillaea lanulosa, Potentilla etomentosa, Mimulus primuloides,* and *Ceanothus cordulatus* fringing the meadow. Snow begins falling about September 15 and usually covers the area permanently from November 15 to May 15, frequently reaching a depth of over 2½ meters. Bright sunny days are much more common than cloudy days even in winter. Rarely in summer there are thunder showers. Frosts occur occasionally even in the summer months. High winds sometimes come in late autumn and in winter.

Methods

All of the pocket gophers on the areas were studied intensively during the snowless months with occasional mid-winter observations. Each animal was live trapped as often as possible, toe marked, and released at the point of capture. Each time it was weighed, the exact location of each capture was noted on a map of the meadow, the condition of its sex and pelage was also noted. Special efforts were made to disturb the environment as little as possible. Ten live traps of the modified Scheffer type (Ingles 1949b) were kept set during the day only (to avoid freezing at night) throughout the season. No bait is required for this trap and not infrequently some animals repeated as many as 15 times in a season. The traps were set at fresh workings at the periphery of the burrow systems in order to ascertain the size and limits of each home range. At the end of late autumn the area enclosed by the pegs set at the limits of the different home ranges was calculated for each home range. The areas were calculated only for certain selected ranges for the first two seasons, after which, only the linear distance across the longest diameter was used for selected typical home ranges. College meadow was intensively studied in 1947–1948 with occasional sampling in 1949 and 1950. Mule Deer Meadow was sampled in 1947 and carefully studied from 1948 through 1950.

Habitat

The mountain pocket gopher spends practically all of its life under ground or under snow. Its preferred habitat is the deep rich soil at the margins of mountain meadows. During the snowless months evidence based on fresh mounds indicates they may be active at all hours but activity is greatly increased between 6:00 and 9:00 A.M. and between 4:00 and 7:00 P.M. The seasonal movements this animal makes with respect to snow and ground water have already been reported (Ingles 1949a). Some animals may be found in the shallow relatively poor gravelly granitic soils on the mountain sides far from permanent water. Frequently these represent isolated individuals that utilize the snow cover in winter to find new home ranges and water and doubtless account in part for the unmarked adults that occasionally reach the meadows by burrowing through the snow.

Home Range and Nests

The concept of "home range" used here is the same as that described by Burt (1940) and is synonomous with "burrow system." There is no evidence that the home range of a pocket gopher is any greater area than that constituting its territory. The mountain pocket gopher is a solitary animal. At no time were two animals taken on the same home range during the same year. Some of these burrow systems were close to others but when trenches were dug between them it was shown that they were never continuous. In one case where a juvenile female was living next to an adult male, a trench 9 meters long revealed the two home ranges were always separated by at least a 120 centimeter corridor, which was crossed by only one fully plugged burrow. It is thought the animals hear each other digging and do not encroach upon the

home ranges of one another. Because they approach each other closely, however, the only accurate means of determining the limits of their home ranges is by live trapping. Measurements and correct identity of burrow systems based on surface work are inaccurate where the burrow systems are closely associated.

Over the three-year period the two acres which were dry enough for gopher occupancy were found to support 24 separate home ranges in Mule Deer Meadow. These were never all occupied in any one year; for example 19 were occupied in the autumn of 1949 and only 10 in the spring of 1950 (table II).

The occupancy of a particular home range site is apparently a matter of chance. The juveniles leave the home nests about the middle of July and disperse over the surface until suitable areas are found. Frequently they settle on areas that are too small, such as an insufficient plot of higher ground surrounded by water-soaked earth. Sometimes the area selected becomes too wet for occupancy the following spring and the animal is forced to move before the snow has melted (Ingles 1949a). Of 9 adult males on Mule Deer Meadow 5 changed home ranges while the snow still covered the ground and 4 remained on the same home range 2 or more years. Of 10 adult females 9 occupied the same home ranges for at least 2 years and 3 were on the same area after 3 years. Only 1 female changed home ranges in the 3 year period. This particular animal was alone on an "island" of dry land near the middle of the wettest part of the meadow in 1948. The next spring, summer, and autumn (1949) she occupied a new home range at the margin of the meadow 37 meters farther west. She reached her new location by going through the snow over a permanent stream after her old range became too wet early in the spring. The next spring (1950) she was again back on the "island" and by autumn a juvenile had also established its home range there. The longest distance traveled by an adult male to a new range was 37 meters (120 feet) and by a juvenile was 120 meters (400 feet). The 5 males which changed home ranges in the winter all moved up grade. However, one of these that reached the woods moved back again in late June.

Each home range radiates from the nest site which is located underground in summer and may be located in the snow in winter. One of the underground nests was opened in midwinter (January 27, 1948). It was 25 centimeters below the surface of the unfrozen earth beneath the roots of a small lodgepole pine. This nest was 25 by 23 centimeters across (viewed from above) and was 20 centimeters deep. Five separate burrows radiated from the nest cavity. The parts of 2 species of plants constituted the bulk of the nest which weighed 657 grams. One of these plants was a finely shredded unidentified grass and the other was represented by the husks of the corms of *Triteleia ixioides* var. *analina*. No fecal or food deposits were found near the nest.

Each spring the melting snow always exposed a number of winter nests made in the snow. There was always a cone-shaped cavity 60 or 90 centimeters long melted in the snow directly above the nest. These nests are very frequently built over soil, which is extremely wet in the snowless months, on fallen logs, or well up in the snow itself. They were always constructed of finely shredded dead grasses, probably the by-products of winter food, and were about the size of the underground summer nests. Almost always a fecal deposit containing thousands of oval black pellets was located nearby. Eight of these snow nests were located on Mule Deer Meadow in the spring of 1950. It seems unlikely that the pocket gophers that live in the snow nests ever find their way back to their summer home ranges unless the nests are constructed directly above them. When the melting snow leaves the animals stranded on water soaked soil they are forced to expose themselves to their enemies while searching for a new home. The best-located

TABLE I. *Showing the sizes of certain home ranges in square feet and others in linear feet for the adults of both sexes and for juveniles from both areas*

	Adult females		Adult males		Juveniles	
	Area (sq. ft.)	Linear (feet)	Area (sq. ft.)	Linear (feet)	Area (sq. ft.)	Linear (feet)
Number examined	13	17	6	12	19	24
Range	90–2,016	20–72	80–1,488	10–120	92–1,886	12–90

summer home ranges are seldom abandoned during winter. The animals that inhabit them may burrow and feed extensively over them or under them and through snow but they always maintain the underground nest connections.

Unlike the nest built in the snow, which were free of commensals and parasites, the underground nests represent a microhabitat for numerous species of arthropods, some of which apparently live there permanently while others live there only during the winter months. Some of these invertebrates live on the pocket gophers and others live in the nest or are found in the burrows. Those living on the animal as parasites are: *Trombicula californica* (mite); *Euhaemogamasus* sp. (an undescribed mite); *Dactylopsylla comis* (flea); and *Dactylopsylla franciscana* (flea). Those that are associated with the nest and burrows are: *Hesperochernes* sp. (pseudoscorpion); *Parasitus* sp. (mite); *Macrocheles* sp. (mite); *Pegomyia duplicata* (dipteran); *Aphodius* sp. (undescribed scarabaeid beetle); *Hister* sp. (undescribed hister beetle); *Trogoderma sternale* (dermestid beetle); *Ptomaphagus californicus* (silphid beetle); *Ptomaphagus* sp.; *Megaguedius explanatus* (staphylinid beetle); *Megaguedius* sp. (undescribed); *Omalium* sp. (undescribed staphylinid beetle); *Aleachara* sp. (staphylinid beetle); and *Sinella* sp. (undescribed springtail). Groups present in which other genera or species have not yet been determined are: Chelonethida, Belbidae, Aleocharinae, Phoridae, Itonididae, and Therevidae.

Fifty-six burrow systems were studied to determine the size needed by the juveniles and adults to provide the necessary requirements of the species. These home ranges were determined by live trapping the animals that lived in them. Because so many of the burrow systems are more or less linear a measure of the greatest distance across them gives a better comparative picture than a comparison of the areas. Areas only were recorded in 1947–1948 and only linear records were made in 1949–1950.

The size of the home range is related to the length of time it has been occupied, the available space, and whether or not it is established over an old burrow system. Frequently a juvenile establishes itself in a previously occupied home range in which many old burrows already exist and in a short time has a large home range. Because of these factors the size of the home range appears to be about equally variable for all of these age and sex groups (Table I). The coefficients of variation were not calculated because both sexes of adults and juveniles were frequently known to occupy old established home ranges.

FOOD

The amount of food available is related to the size of the home range. A pocket gopher that moves on to a previously occupied area needs only to renovate several linear feet of old burrows and has immediately available plenty of food with relatively little effort, as compared with one that must dig its way to the growing roots and corms in a new area. Rarely has an area been so thoroughly worked as to exhaust the easily available food. The mountain pocket gopher eats several of

the plant foods previously listed. During the snowless months caches of corms and roots of *Lewisia nevadensis* and *Tritileia ixioides* var. *analina* have been found in special underground cavities 25 to 30 centimeters in diameter. In winter large caches of leaves of *Ceanothus cordulatus* have been found in the snow. Most of the food in summer is obtained from the roots growing down into the tunnels or is reached by digging new tunnels. In winter the greater part of the food comes from the green stems of grasses and sedges which the animal gathers as it extends its burrows under the snow. Sometimes areas of 100 square feet or more are almost completely denuded of vegetation along the winter burrows made under the snow. The dead ends of these plants are pushed into unused burrows sometimes forming plugs under the snow many feet in length. Frequently the bark of willows (covered with snow) is gnawed off many inches above the ground. The amount of food eaten each day by a pocket gopher is not known.

Reproduction

Unlike the species living in the San Joaquin Valley in which the mating instincts are best developed at the time of year when the soil is most tractable and the green vegetation is best developed (Miller 1946) the mountain pocket gopher breeds while the ground is too wet for digging and there is practically no green vegetation in evidence.

Three females taken between May 13 and 29 each had the vulva greatly enlarged indicating that the rutting season is well advanced even before the snow melts. The gestation period is not known. The sudden loss in weight of a few large females indicates that parturition occurs between July 20 and August 10. One animal 3 years or more old had long teats and 4 half-grown embryos on July 20. Uterine scars on other females indicate a litter size of 3 or 4 young. Live trapping results indicate but one litter a year for this species as compared with an average of 2 for *Thomomys bottae* (Miller 1946). None of the 18 females caught while lactating showed a second lactation the same season, although some were taken as many as 15 times in the season in the live traps. Females will breed the year after they are born. Dispersion begins the middle of July and continues until September 1. Twelve juveniles weighing between 30 and 58 grams started establishing new home ranges of their own on Mule Deer Meadow between August 16 and September 2. Juveniles are not in evidence at any other times of the year, indicating but a single litter per year.

The weights of juveniles representing the rate of growth of this species were previously reported (Ingles 1949c). It was noted that the animals emerge from winter weighing more (spring averages) than they do in the other seasons when

Table II. *Showing population, average weights (in grams) and animal mass per acre for 1947 (College Meadow only) and 1948–1950 (Mule Deer Meadow only)*

	College Meadow				Mule Deer Meadow					
	1947	1948			1949			1950		
	Autumn only	Spring	Summer	Autumn	Spring	Summer	Autumn	Spring	Summer	Autumn
Animals per acre	14.5	8.0	14.0	10.0	9.0	19.0	10.0	10.0	4.0	4.0
Av. weight per animal	73.6	88.1	62.5	73.0	75.1	69.6	75.0	87.1	82.7	86.5
Animal mass per acre	1,068.0	704.8	875.0	730.0	674.9	1,322.4	750.0	871.0	338.0	346.0

surface vegetation is at its height (Table II).

The number of animals per acre and their total weights were calculated for each of the 4 years (Table II).

The average population per acre in autumn is near 10 animals which is more than twice as many as was found for *Thomomys bottae* in the mountains at Bass Lake (Storer *et al.* 1944) but only half as many as were in the uncultivated land of the San Joaquin Valley (Ingles *et al.* 1949). Mohr (1947) compiled figures for *Thomomys talpoides* as follows: "number per acre 2 to 10; individual weights, 140 grams; and grams per acre, 280 to 1400." The drier conditions of College Meadow seem to favor pocket gophers more than do the permanently wet conditions of Mule Deer Meadow. The drop in population on Mule Deer Meadow in summer and autumn of 1950 is unexplained.

The mass of the population was 12% greater in summer (July-August) when the vegetation was at its height than in the spring (May-June) (Table II). Twenty-seven animals on Mule Deer Meadow in the spring months 1948–1950 averaged 83.3 grams; 37 animals in the summer months averaged 68.5 grams in the same years (Table II). During the four year period 82 animals were marked on the two meadows (total 4 acres).

Only 4 females are known to have lived 3 or more years. Three of these were adults when marked and therefore were at least 4 years old when last trapped. It is doubtful if any live to 5 years of age. Eight males and 15 females are known to have lived 2 or more years on the meadows.

When these data are applied to the formula for estimating average longevity (Petrides 1949) the result is

$$L = \frac{1}{j} = \frac{1.0}{.34} = 2.9 \text{ years},$$

where L is average longevity, J is the proportion of young animals in the autumn population (see Table III). This figure seems somewhat too high when compared with trapping experience. It would of course, be lower if data were available for late winter.

TABLE III. *Showing autumn population composition of both stations*

	1947	1948	1949	1950	Average
No. of animals trapped	36	35	21	13	26.2
Female adults	44%	40%	38%	38%	40.0%
Male adults	20%	28%	24%	31%	26.0%
Juveniles	36%	32%	38%	31%	34.0%

Only one adult breeding male came to Mule Deer Meadow in the spring of 1949 to join the 4 adult males that were raised there. In the spring of 1950 one adult female and one adult male, not raised on the area, joined the potential breeding population of 4 adult females and 3 adult males. These potential breeders probably came from other colonies from 100 meters to 500 meters down stream or from the mountain side. The pocket gophers in these two meadows are relatively isolated from other colonies and probably are representative of the type of distribution of the species as a whole. In such small breeding populations one could expect to find mutations becoming fixed which would serve to make populations significantly different as has already been shown to be the case with *Thomomys bottae* (Ingles, 1950). The relatively high per cent of "new breeders" here would probably tend to prevent this fixity of mutations by increasing the genetic heterogeneity of the colony. Whether some of the thousands of relatively isolated populations of *Thomomys monticola* actually differ significantly from others would be worthy of investigation. The colonies of this species are much smaller, are much more isolated, and there are fewer chances for emigration than with those of *T. bottae* where such differences in certain populations are known to exist.

The composition of the population expressed as percentage remained rather constant even though the actual numbers

varied from year to year. After the juveniles become settled in their own home ranges they constitute approximately one-third of the population (Table III).

It seems most likely that the period of greatest vulnerability is in late spring when the melting snow and rising ground water force the animal to seek new underground burrow systems on higher and drier ground. Such an animal moving across the surface of the snow must certainly be conspicuous to any predator.

Parasites and Predators

No study of the internal parasites has been made of the mountain pocket gopher. They are known to harbor a species of unidentified nematode in the caecum which resembles the genus *Trichuris*. Besides the parasitic mites and fleas and those species previously listed as living in the underground nests no other associates are known. In the spring some of the animals become so heavily parasitized with mites that the ears, genitalia, and lips have an orange color. These do not appear to affect the animal's health.

Potential predators that have been seen, heard, or otherwise known to live in the woods surrounding the meadows are striped skunk, coyote, mountain weasel, goshawk, red-tailed hawk, spotted owl, and horned owl. Of these the horned owl is the most commonly observed at all seasons.

Pelage

The condition of the pelage was noted each time an animal was captured and some information was gained on the moult that occurs in the summer and autumn months. This moult starts on the head and moves back over the body of adults as a visible ring around the body. This ring, which is more obvious as the winter pelage gives way to the summer pelage, resembles a minature horseshoe lying over the back with the ends somewhat more anteriorly placed along the sides. The new brown short summer pelage thus replaces the grayish blue winter pelage rather rapidly until the ring reaches the lower hip region where it often remains for 3 or 4 weeks before going to completion. This moult generally begins in the first part of August and is over by the middle of September. No moult lines were seen in October and only rarely were any observed in July.

The juvenile bluish gray pelage is apparently only rarely moulted regularly as a ring progressing down the body, but instead the fur comes off in large irregular patches as it is replaced by the winter pelage. This juvenile moult begins in August on some individuals and does not start on others until October or November. The resulting pelage resembles the adult summer pelage except that it is finer. A few adult individuals taken in January and early April were in winter pelage and nothing was learned regarding the time and manner in which this pelage was acquired.

Economic Considerations

Because the mountain pocket gopher lives in the high mountain meadows it is not a pest to agriculture as are related species occupying cultivated lands at lower elevations. It is very probable that further study will demonstrate this species is actually a benefit economically as has been suggested by Grinnell and Storer (1924) and by Grinnell (1933). Such a study should be carefully conducted in the field experimentally over a much longer period of time than was available here.

This species of pocket gopher does exert pronounced effects on its environment and some of these were superficially studied. It was found that surface mounds were only occasionally made in May and June but were common in July and reached their maximum development in August and September. During these latter months it was found that an average of 45 kilos (100 pounds) of earth were brought to the surface every 8 days over each of 10 burrow systems studied (5 on each area). With an average of 10 ani-

mals per acre approximately 4.2 metric tons per hectare or 1.9 English tons of mineral earth per acre were brought to the surface each month including July through October to be mixed with vegetative materials. The annual amount of soil moved, over 7½ tons per acre per year, represents much more than that found by Ellison (1946) who worked with *Thomomys talpoides morrei* in the mountains of Utah. He estimated 5 tons of earth were brought to the surface per acre per year. Buechner (1942) calculated 7.08 tons per acre per year for *Geomys breviceps brazensis* in Texas which would still be less than that brought to the surface during the 5 or 6 snowless months on these meadows. The "cores" which are formed in and under the snow (for photographs see Grinnell 1933) indicates that this activity continues all winter, though probably at a reduced rate. Unlike the mounds of the species living at lower elevations, which frequently cover up grass, the summer mounds of this species are rarely in evidence after the thaw the following spring. By this time they have been washed away or reduced to such an extent that the underlying grass easily grows through the soft earth.

The close browsing of the grasses and sedges under the snow may possibly do damage to grazing interests although the plants are not killed by it. In Utah and Texas (Ellison 1946; Buechner 1942), where different species of pocket gophers were studied in relation to soil erosion and grazing, the conclusions were that the pocket gophers had little appreciable effect on either. The numerous fecal deposits about the nests made in the snow undoubtedly have a beneficial effect on the vegetation. Storer (1947) says that on wild land gophers may be beneficial in the long run.

The burrow systems are important in that they allow the heavy surface runoff each spring to sink underground. On Mule Deer Meadow the only places where the spring runoff went underground was over the burrow systems. Because the soil over these systems also dried out sooner each summer, grasses instead of sedges grew there. There is no evidence that gulley forming or excessive erosion results from pocket gopher activity in these meadows. Ellison (1946) came to similar conclusions regarding the effects of *Thomomys talpoides* in the mountain meadows in Utah. Except where environmental conditions are similar evaluations of economic status or the effects of an animal on its environment are useless. Such evaluations should be made only after critical experimental studies that have been conducted over a period of several years in the field.

Summary

1. The ecology of the mountain pocket gopher was studied over a 4 year period in two mountain meadows in the Sierra Nevada Mountains near Huntington Lake, California.

2. All of the animals were live trapped and marked in order to study home range, weight, parasites, moult, and population.

3. The mountain pocket gopher is solitary and maintains a home range that is not connected with that of another animal.

4. A home range consists of a system of underground or under-snow tunnels that radiate from underground or under-snow nests made from the inedible parts of plant foods. The size of an underground home range varies from 7.4 to 187 square meters (80 to 2016 square feet) or 3 to 37 linear meters (10 to 120 feet); those under snow are known to be larger. The nests are microhabitats harboring many species of arthropods, many undescribed.

5. Food is frequently cached. Besides the roots, bulbs, and corms, growing along the burrow system, which are eaten at all times of the year, the stems of grasses obtained from burrows under the snow provide most of the winter food. Leaves and bark of shrubs are also eaten in winter.

6. The average weight is between 62.5 and 88.1 grams for adults. They weigh

more at the close of winter than they do in the snowless months. The total mass varied from 836 to 2,640 grams per hectare (338 to 1,068 grams per acre) depending on the season, year and station.

7. Approximately one-third of the population in autumn consists of juveniles; 20% to 31% are males; 38% to 44% are females.

8. Average longevity is less than 2.9 years and population turnover is complete between 4 and 5 years.

9. The relatively small interbreeding population is augmented each year by one or two potential breeders from other areas, which presumably prevent to a considerable degree any genetic drift of new mutations to fixity in the population.

10. The period of greatest vulnerability is probably in the late spring when the snow melts exposing the winter nests and the snow burrows built over water-soaked ground.

11. One nematode, two mites, and two fleas are known as parasites of the animal. Only probable predators are known.

12. The moult to summer pelage begins the first of August and is over by the middle of September.

13. There is no evidence that the animal is harmful to grazing interests. On the contrary there is considerable evidence that the species is beneficial as a soil builder and a conserver of water.

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THE EFFECTS OF SOLAR RADIATION ON GRASSHOPPER TEMPERATURES AND ACTIVITIES [1]

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Introduction

The importance of the physical environment and its effect on animal behavior and development has been recognized by biologists for many years. Among the earlier studies to be made were those involving insect metamorphosis and activity in relation to moisture and temperature. Light as an environmental factor was first considered in relation to its effects on choice or habitats and orientation. Later, when the relationship between insect body temperature and light became more generally recognized, studies were initiated to determine the importance of light in modifying body temperatures.

Gunn (1942) reviewed the more important studies on the body temperatures of poikilothermal animals and the factors which influenced these temperatures. He also discussed in some detail the qualitative and quantitative aspects of radiant energy and the laws governing its behavior.

Such factors as the quantitative and qualitative composition of radiant energy, convection, conduction, radiation, evaporation, metabolism, and body form and composition all contribute to the equilibrium temperature attained by the poikilothermal animal. In order to measure and accurately interpret the effect of an individual factor on the body temperature of a poikilotherm, it is necessary to have an understanding of the underlying phenomena of heat transfer, and to consider the interrelations between factors in taking the experimental data.

Gunn (1942) pointed out that conduction and convection were complementary processes that tend to equalize the body temperatures and the temperature of the immediate surroundings. Heat is passed by conduction between the insect's surface and the thin layer of air in contact with it, while convection assists in the prior or later movements of heat toward or away from this thin layer. There must be some conduction of heat between an insect and any solid surface with which it may be in contact. In air, if convection can be prevented, conduction is responsible for little heat transfer; stationary air is a good heat insulator.

Objects are known to differ in their ability to absorb different portions of the radiant energy received from the sun. Burkholder (1936) stated that the quality, intensity, and duration of solar radiation at any point on the earth's surface varied in a definite manner with the time of year, altitude, and latitude, and might be modified, further, by atmospheric absorption and scattering and by local obstructions due to topographical features, plant formations, etc. Energy of different wave lengths also varies in the extent to which it is differentially absorbed by the atmosphere. He likewise stated that approximately 60 per cent of the total radiation of the sun was composed of infra red. These rays vary in intensity depending on atmospheric conditions and are reflected and absorbed to varying degrees depending upon the character of the surface. Without having a knowledge of the energy being received and that which is reflected, the effectiveness of the surface as an absorbing system cannot be truly ascertained.

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A quantitative measurement of the total radiation will provide no information on the composition of the energy being received.

A cold blooded animal can act both as an absorbing and as a radiating body. It will absorb radiation from the sun's rays as well as from other objects in its immediate surroundings. The rate of heat exchange will be determined by the character of the radiating bodies as well as by their relative temperatures. If an insect is a poor conductor of heat and is not receiving any radiation, it may have a body temperature lower than that of its surroundings because it radiates heat at a greater rate than it receives it by conduction.

Evaporation of body fluids as a factor in modifying the body temperature of some insects has been pointed out by numerous workers. Wigglesworth (1945) in studying the water loss in a number of insects, found that those which normally live in a high moisture environment have less resistance to water loss through the exoskeleton than those inhabiting a drier environment. Chefurka (1949) in studying the rate of water loss by evaporation through the exoskeleton of *M. bivattatus* found that the rate increased considerably at or above the critical temperature of the wax which forms the outer portion of the exoskeleton. He found this critical temperature to be 44° C. which approaches the extreme limits of temperatures encountered by grasshoppers in their natural habitat.

As water is lost by evaporation, heat is removed; but, at the same time, heat may be supplied continually to the organism by conduction, convection, radiation, etc. The rate of water loss is controlled, to a large extent, by the properties of the wavy coating over the exoskeleton and the rate of heat gain by the factors stated above. The amount that the body temperature is lowered will be determined by the ratio of this heat loss to gain. This ratio may differ considerably between insects, inasmuch as their ability to absorb energy is subject to factors which will vary widely between species. Where the influence of radiant energy is measured by its effects in increasing the body temperature of an insect, the results will be influenced by the nature and extent of the surface area exposed. The ability of an object to absorb radiant energy striking its surface is determined by the reradiating properties of the surface. A smooth, shiny surface which readily reflects radiation will absorb less of it than a surface that does not reflect to the same degree. Gunn (1942) pointed out that the properties of the surface affected the amounts of the various components of solar radiation that were absorbed.

Buxton (1924) and Hill and Taylor (1933) reported a difference in body temperature between dimorphic forms of locusts (black and pale green or buff) when they were exposed to the same degree of sunlight. These locusts were exposed to intensive reflected radiation (earth and surrounding objects) as well as direct radiation from the sun. Color alone cannot serve as a true indicator of the absorbing qualities of a surface because a color merely indicates that some part of the energy in the visible spectrum is being reflected instead of being absorbed.

The ratio of surface area to volume and the general composition of the insect tissues would, in all probability, modify the temperature response to solar radiation.

Certain insects, during periods of great activity, are known to raise their body temperatures by their metabolic processes. However, metabolic activity in quiescent species could be expected to have much less effect on these body temperatures.

The studies reported in this paper are concerned with the measurement and evaluation of some of the various factors involved in the maintenance of body temperatures in grasshoppers. In order to make these studies, it was necessary to employ specialized techniques, whereby controlled conditions could be obtained,

thus eliminating, as far as possible, additive or interfering effects from factors other than those being evaluated.

Experimentation

A non-reflecting light cone of the kind employed in radiation research was used in determining the effect of direct solar radiation on grasshopper body temperatures. Unless otherwise stated, all temperature data reported herein were obtained by the use of this equipment. This cone was a type of "black-body" or "Hohlraum" which provided a background independent of everything but the temperature of the cone. Ruark and Urey (1930) adequately discuss the theoretical considerations in the use of the black-body in radiation research.

The modification of the black body which was used in this work was constructed of tin, cone-shaped, and curved. The inner surface of the cone was coated with lamp black in shellac. This black-body was suspended inside a plywood box; thus, shade was provided for all but the opening in the upper end of the cone. The plywood box was set on a dais and provided with a sighting arrangement so that this opening could be oriented toward the sun. An Eppley pyrheliometer was mounted on the plywood box adjacent to the opening in the black-body. The arrangement was such that a grasshopper could be suspended inside this small opening in the upper end of the cone. A grasshopper so placed was subjected only to direct solar radiation of a measured intensity.

The grasshoppers were exposed to a minimum of convection and conduction effects, as was evidenced by the fact that the air temperature within the black-body rarely increased more than 0.5° C. during the time measurements were being made. All temperature measurements were made using copper-constantan thermocouples which were constructed from 0.005 in. diameter wires and specially treated and wrapped to insure complete insulation. In calibrating the thermocouples, no thermal conductance along the wires could be detected.

The sunlight intensity was measured with an Eppley pyrheliometer, calibrated in gram cal./sq. cm./min. All potentials including temperature measurements were obtained with a Leeds and Northrop type K potentiometer adapted for field use. All equipment for the radiation studies was adapted for field use and the measurements were made on the site where the grasshoppers were collected.

Silk thread was used to suspend the grasshopper within the black body in such a position that a maximum of the insect's lateral surface could be exposed at right angles to the direct rays of the sun. One thermocouple was placed in the grasshopper and another, shaded from the direct rays of the sun, suspended in the air immediately surrounding the insect. The aperture through which the sunlight was allowed to enter the black-body was closed and left so until the temperature of the grasshopper and that of the air surrounding it became constant. Without exception, the two temperatures at this time were identical. The direct sun's rays were then allowed to strike the surface of the insect and measurements were taken at various intervals of time until no further rise in body temperature was noted. The time required to reach a constant difference between air and body temperatures was found to vary between 10 and 40 minutes, depending upon the test insect, the air temperature, and the sunlight intensity. It required approximately one minute to make a determination of the grasshopper temperature, the temperature of the air surrounding it, and the light intensity.

Since only one side of the grasshopper was exposed to solar radiation, the temperature gradient across the insect's body was investigated. Three thermocouples were inserted in the metathoracic sternum, one just beneath the cuticle on the exposed side, another at the mid-line, and the third just beneath the cuticle on the shaded side. Identical readings were ob-

tained from all thermocouples before exposure. Temperature readings were taken at various intervals at the three sites after the test insect was exposed to the sun's rays.

In adult *Melanoplus bivittatus* (Say) having a metasternal width of 8 mm., the temperature difference between the two sides varied between 3.5 and 4.7° C., while in those with a width of 5 mm. the difference was 3.2° C. With *Melanoplus mexicanus* (Saussure) having a width of 4 and 2.5 mm., the differences were found to be 2.5 and 1.2° C., respectively. The temperature taken at the mid-line never was found to be intermediate between the two temperatures taken at the lateral surfaces, but was found to be approximately 1° C. higher than that of the non-radiated side.

It is apparent that only when the grasshopper is receiving radiation equally from all sides or when it is in complete darkness will the temperature obtained in the center of the thorax be the true temperature of the test insect. It was felt that, since the temperature of the grasshopper would never be uniform throughout, except under the conditions stated above, the best measurement for comparative purposes could be obtained by always taking the temperature at the same place and in the same manner. The mid-line of the metathoracic sternum was selected as the place in which all subsequent temperature readings were taken.

Many statements have been made to the effect that insect body temperatures may be lowered by the evaporation of body water. The effect of this water loss was determined for *M. bivittatus* in the following manner: The insect was placed in a darkened tube through which dry air passed at a velocity of 10 miles per hour. When a constant and desired temperature was obtained within the chamber, a grasshopper with a thermocouple inserted in it was suspended in the tube at right angles to its long axis. Air and grasshopper temperatures were taken until the difference between them became constant. At room temperature, 25° C., no appreciable difference could be noted between the air temperature and the grasshopper's temperature. At an air temperature of 39.1° C., the grasshopper's temperature reached a constant value of 38.2° C. or 0.9° C. lower. When the air temperature was adjusted to 49.4° and 54.9° C., the body temperature was 2.0° and 3.2° C. lower, respectively, than the air temperature. These data show that, even under the extreme conditions of the experiment, only minor temperature effects could be noted through the loss of body water in this grasshopper species.

In the tests already discussed, as well as in all subsequent ones, when the insect was immobilized and suspended in the black-body with all radiation excluded, the body temperature of the grasshopper always was found to be the same as that of the surrounding air. Therefore, it was concluded that, under these conditions, no appreciable temperature effects from metabolic heat, conduction, convection, or evaporation could be expected. With the above factors having been evaluated and being able to eliminate all reflected light by the use of the black-body, it was then possible to evaluate the temperature effects of direct solar radiation.

Using the black-body technique, the rise in body temperature due to direct solar radiation was investigated for three species of grasshoppers. Determinations of body temperature, surrounding air temperature, and light intensity were continued until the temperature difference between the insect and the surrounding air became constant.

Twenty uniformly yellow-colored specimens of female *Melanoplus differentialis* (Thomas) of like size were tested under different light intensities and air temperatures. All values for light intensity are expressed in gram cal./sq. cm./min. The variations in air temperature and light intensity for this series of tests were from 16.1° to 40.7° C. and from 0.13 to 1.36 gr. cal., respectively.

The average rise in body temperature

per gr. cal./sq. cm./min. of radiation was 8.1° C. for the 20 specimens. In 13 of these the rise was between 7° and 9° C. per gram cal. The extremes were 4.6° and 13.6° C. per gr. cal. At approximately the same light intensity, the degree rise in body temperature per gram cal. was highest at the lower air temperatures. In this series of measurements the average actual increase in body temperature above that of the surrounding air was 8.1° C., the greatest increase being 12.0° and the lowest 1.8° C.

Ten adult black *M. differentialis* were also subjected to the above test and the results, when compared under the same conditions of air temperature and light intensity, were not significantly different from those obtained using the yellow forms. The average rise in body temperatures per gr. cal./sq. cm./min. was 7.6° C. The variations in air temperature and light intensity were somewhat less than in the series involving the yellow forms, the light intensity ranging from 1.16 to 1.37 gm. cal. and the air temperature from 23.5 to 41.3° C. The average actual increase in body temperature above that of the surrounding air was 9.7° C., the greatest being 12.2° and the lowest 8.1° C.

Several determinations were made where one each of the dimorphic forms (black and buff) of *M. differentialis* nymphs were suspended side by side in the black-body and exposed to direct solar radiation. The dark forms always reached a constant temperature more rapidly than the light ones, but within the total exposure time of 20 minutes both forms reached and remained at approximately the same temperature (± 1.0° C.) throughout the observation period.

Further tests were conducted using 25 adult female *M. bivittatus*. In these tests the air temperature varied from 31.5° to 41.7° C. and the light intensities from 0.88 to 1.36 gr. cal. An average value of 6.7° C. rise in body temperature per gr. cal./cm. sq./min. was obtained. The extremes were 4.6 and 8.2° C. rise per gram cal. As was the case with the previously mentioned species, the rise per gr. cal. in body temperatures of *M. bivittatus,* at the same level of light intensity, was the highest at low air temperatures. The average actual increase in body temperature above that of the surrounding air was 8.1° C., the greatest increase being 11.2° and the least 4.1° C.

In another series of experiments involving 15 determinations, the effect of direct solar radiation on *M. bivittatus* and *M. mexicanus* was compared. A specimen of each species was suspended in the same plane in the black-body, one above the other, but not in contact with each other. In this series of tests, the air temperature varied from 31.5° to 41.4° C. and the light intensities from 0.88 to 1.32 gm. cal.

The average rise in body temperature per gm. cal./sq. cm./min. obtained for *M. bivittatus* was 6.7° while that obtained for *M. mexicanus* was 5.9° C. The average actual increase in body temperature above that of the surrounding air was 8.1° and 7.1° C. for *M. bivittatus* and *M. mexicanus,* respectively. The greatest increase in *M. bivittatus* was 10.3°, the least 4.1° C., and the greatest in *M. mexicanus* was 8.9°, the least 3.4° C. The limits of light intensity and air temperature encountered in conducting this series of tests were almost identical to those met with in the series of measurements described above where *M. bivittatus* were used alone. It will be noted that the averages for the degree rise per gm. cal./cm. sq./min. were the same for the *M. bivittatus* species in the two series of tests.

In order to evaluate, under field conditions, the effects of temperature factors other than solar radiation, the body temperatures of 80 *M. bivittatus* in their natural habitats were obtained. Their positions varied from the insects being in complete shade to their being completely exposed to sunlight. All the factors, including solar radiation, were presumably operating. In each case the grasshopper body temperature was above that of the air. These increases were found to vary

TABLE I. *Response of the various species of grasshoppers to direct solar radiation as determined by the black-body technique*

Species	Limits of light intensity (gr. cal./sq. cm./min.)	Limits of air temp. ° C.	Actual increase in body temperature ° C.		Rise in body temp. per gr. cal./sq. cm./min. ° C.	
			Average	Limits	Average	Limits
M. differentialis (yellow forms)	0.13–1.36	16.1–40.7	8.1	1.8–12.0	8.1	4.6–13.6
M. differentialis (black forms)	1.16–1.37	23.5–41.3	9.7	8.1–12.2	7.6	6.2–10.5
M. bivittatus (series of 25)	0.88–1.36	31.5–41.7	8.1	4.1–11.2	6.7	4.6– 8.2
M. bivittatus	0.88–1.32	31.5–41.4	8.1	4.1–10.3	6.7	4.6– 8.0
M. mexicanus (simultaneous determinations)			7.1	3.4– 8.9	5.9	3.4– 8.9

between a minimum of 0.5° and a maximum of 11° C. The average rise in body temperature of this same species, when exposed in the black-body to only the direct radiations of the sun, was approximately 8.0° C.

The data presented in the foregoing paragraphs will be found summarized in Table I.

DISCUSSION

The data presented in this paper should help to clarify some of the controversy which frequently arises with regard to the taking and interpretation of temperature data in connection with ecological studies on grasshoppers. These data point out the need for isolating and studying separately each factor which may contribute to the ultimate body temperature.

There is a lag in heat transfer from the radiated to the non-radiated side of the grasshopper. This was shown by placing a series of thermocouples across the thorax. The lag in response was influenced by the width of the thorax. It is apparent that when the grasshopper is being exposed to radiation from only one side, the temperature of its body is not uniform throughout.

In *M. bivittatus* the removal of heat by evaporation of water from the body surface appears to be a minor factor in modifying the body temperature. Only under extreme conditions, involving completely dry air and temperatures above 40° C., could this water loss be of any significance in determining the resulting body temperature.

No significant differences due to coloration were noted in the body temperatures of dimorphic forms of *M. differentialis* when they were subjected to direct solar radiation only. This was evident when comparisons were made between the two forms under the same conditions of air temperature and light intensity. While the average actual increase in body temperature was found to be 1.6° C. higher for the series of black forms than for the series of yellow ones, it will be noted that the light intensities under which the responses were measured were considerably lower for the series of yellow forms.

In the species of grasshoppers studied, the insects' body temperatures always assumed that of the surrounding air inside the black-body before exposure to the sun. This fact is evidence of the lack of effect of metabolic heat in body temperatures of these species when quiescent. It is possible, however, that under conditions of extreme activity such as active flight (migrations) metabolic heat might

become a contributing factor to body temperature.

In their natural habitat the rise in body temperatures of grasshoppers above that of the immediately surrounding air theoretically results from obtaining energy from several different external sources. The sources which might contribute are direct solar radiation, reflected light, heat radiation from surrounding objects, and conduction through contact with objects at a higher temperature. The data obtained show that, under the usual field conditions, the greater portion of the energy which results in raising the body temperature of grasshoppers comes from the absorption of direct solar radiation. Under extreme circumstances, however, field conditions could be such that the higher body temperatures would be more attributable to factors other than direct solar radiation.

It is apparent that grasshopper species differ somewhat in their ability to absorb radiant energy. While the differences between the species studied were not found to be very large, there could be occasions when such differences might affect development and also affect such activities as orientation, migration, feeding, and other behavior phenomena.

The data also show that, in nature, a grasshopper's body temperature may be considerably higher than that of the surrounding air. While the extent of this rise in body temperature may differ considerably from time to time, the accumulative effect over the entire developmental period of the grasshopper may be highly significant. Data obtained in temperature cabinets and translated for field application in terms of air temperatures can lead to erroneous conclusions where the assumption is made that the grasshopper temperature is the same as that of the air.

Fraenkel (1930), in working with the desert locust, reported an orientation of the grasshoppers which he attributed primarily to the action of receptors of radiant heat which are distributed over the entire body. Orientation on the part of many grasshopper species with respect to the sun's rays is a common observation in field behavior studies. It is apparent that, by this process of orientation, these grasshoppers can exert a degree of control over their body temperature which may be highly significant, both from the standpoint of rate of development and general activity.

During the course of this study, the localized movements of *M. bivittatus* and *M. differentialis* were noted. In the early morning, just at sunrise, and during the late evening as the sun is setting, there is a mass movement and orientation of these species with an apparent attempt to expose a maximum of their surface to the direct rays of the sun. This is accomplished by their climbing up on vegetation or other objects. It is not uncommon to observe them making slight changes in their position in order to present previously unexposed areas to the sun. In the late fall when the air temperatures are relatively low, these grasshoppers frequently maintain the above type of orientation throughout the entire day. In view of the possible effects on body temperature which may be brought about by this orientation, it appears that this activity is motivated primarily by a temperature response.

Summary

Studies were made to determine and compare the effect of direct solar radiation on the body temperatures of *Melanoplus bivittatus, M. mexicanus,* and *M. differentialis* in its dimorphic forms. A modification of the black-body was used to obtain the data.

In order to evaluate the data, it was necessary to investigate several possible additive or interfering effects. Included in these were the temperature gradients across the grasshoppers' bodies, heat losses through evaporation of body moisture, metabolic heat, and conduction and convection effects. Under the conditions of the experimentation, most of these factors were shown to have little, if any, in-

fluence on grasshoppers' body temperatures.

The rise in body temperature per gr. cal. per sq. cm. per min. of radiation was found to vary with the air temperature and the light intensity. A difference between species in their temperature response when exposed to direct solar radiation was also demonstrated.

Body temperatures of grasshoppers were determined in individuals in their natural habitat. In all cases the insects' temperatures were above those of the surrounding air. This increase in body temperatures over that of the air, from 0.5° to 11° C., could be accounted for by the action of direct solar radiation. Certain behavior patterns could also be ascribed to a temperature response brought about by this same source of energy.

The actual increase in grasshopper body temperature over that of air brought about by the action of the sun's rays was found to be as much as 12° C. under conditions of low air temperatures and high light intensities. No appreciable differences in temperature response to solar radiation could be ascertained between the dimorphic forms of *M. differentialis* (black and buff).

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NOTES AND COMMENT

AN ANALYSIS OF ECOLOGICAL FACTORS IN THE OCCURRENCE OF CHARACEAE OF THE WOODS HOLE REGION, MASSACHUSETTS[1]

The problem of the distribution of Characeae has intrigued botanists for some time. The fact that these plants may abound in one pool and yet be absent from similar pools in the immediate vicinity, and that a given form may occur in widely separated parts of the continent, has led to conjecture and research in an endeavor to account for the apparent unpredictable nature of occurrence. The fact that under some conditions a species may be markedly transient and in others markedly stable (Wood 1950) adds further interest to the problem.

The question of occurrence can be reduced to three major problems: 1) the method of dispersal, 2) the environmental factors favorable to ecesis, and 3) environmental factors leading to elimination in succession.

The method of dispersal has been generally assumed to be effected by water birds as the major vector in transporting mud containing viable propagules (mainly as oospores) from one water system to another. Olsen (1944: 216 ff.) has reviewed the literature regarding the possible mechanisms of dispersal. As far as is known to the writer, the hypothesis of dispersal by migratory birds has not been critically tested.

The third problem concerning factors leading to the elimination of Characeae in succession, must depend to a large extent upon a knowledge of the factors promoting and inhibiting a characean vegetation. It seems apparent that elimination of a given species could be correlated with changes in any of a number of factors, and when one of the factors changes to such a degree as to become inhibiting would be causal in the elimination of that species.

The second problem, the environmental factors favorable to ecesis, then, is considered to be basic to an understanding of the general problem of distribution; and it is these factors which are the objective of the present study. In order to ascertain the requirements of Characeae, it would be desirable to employ controlled culture techniques; but as yet no satisfactory culture method for these plants has been developed. Attempts to obtain pure cultures by the writer and his associates have met with only partial success. Such attempts have shown Characeae to be delicate organisms, and results would suggest that they may have rather narrow tolerances and specific requirements. In lieu of suitable laboratory procedures, available published information as well as that presented in this study have been obtained through field investigations. The work of Stroede (1931, 1933) and Olsen (1944) assembled valuable data on the tolerances of various European species to environmental factors such as salinity, pH, and hardness. Certain of the species included in those works are also represented in the flora of the United States, but as yet no comparable source of information is available for those American species most likely to be utilized in future investigations. Kiener (1944) in cooperation with Daily (1944) carried out the first American ecological study supported by a knowledge of the taxonomy of the species under consideration. A number of other American studies of aquatic plants have been reported in which "Chara" was included, but as no distinction among the species was made, the information is of little value in the present problem.

A collector specializing in a particular group of plants tends to become well acquainted with the general characteristics of the habitats in which he is likely to find his species, and perhaps unconsciously develops a partial understanding of the probable ecological factors of greatest importance in distribution. The writer had developed some ideas through his experience in collecting Characeae, and had formed certain tentative conclusions as to the relative effect of major environmental factors on the distribution of the members of this group. Data from such observations are subjective to an extent, and the present study was undertaken to provide, if possible, a substantiable body of evidence which might reinforce, supplement, or modify his opinions.

Methods

The method employed to provide a body of evidence which would help establish the relative importance of environmental factors in the distribution of Characeae, consisted of a field survey. During the survey over fifty aquatic habitats in the vicinity of Woods Hole, Massachusetts, were investigated. Rather complete data were ultimately gathered on twenty-six of these, the data for the remainder being insufficiently complete for presentation at this time. Similar studies undertaken by the writer in Rhode Island have, in general, confirmed the results of the Woods Hole survey. The major objectives of the survey were to ascertain: a) *differences* between habitats, one supporting and the other not supporting a given species and b) *similarities* between habitats which supported the same species. The water systems selected were those along a twenty-five mile drive in the vicinity of Woods Hole, and

[1] These investigations were carried out in part through the facilities of the Marine Biological Laboratory, Woods Hole, Mass.

which were sufficiently accessible to allow rapid collection of samples. This was done to reduce the time between collection of samples and laboratory analysis and to thus reduce the amount of change in the samples caused by the action of microorganisms. In order to attempt to reduce the error introduced by this factor, as well as those resulting from changes in the environment from hour to hour during the day, the collections were first made along the route in one direction, and on a later day the sequence of collecting was reversed. By this means it was possible to establish at least the order of the relative intensities of each factor measured that would exist at a given instant among the various habitats. For example, pond A could be shown to regularly have a higher pH value at a given time than pond B, etc., although the pH varies in both ponds throughout the day.

The original survey was run during the summer of 1947, and supplementary data have been gathered during the summers of 1948, 1949, 1950, and 1951. Notes were taken as to the type of water system, bottom, obvious plants occurring in the habitat, and species of any

TABLE I. *Aquatic habitats inspected during survey, data concerning the habitat, and species of Characeae found*

	Habitat	Basin type	Bottom type	Plants	Temp. °C	Alkalinity		pH	NaCl	Characeae
						M.O. ppm	ph-th ppm		0/00*	(*C* = *Chara*, *N* = *Nitella*)
1	Ashumet	lake	sand	*Lobelia*	25	19 25	0 0	6.9 6.5	0.0 0.0	*N. transilis* *N. megacarpa* *N. flexilis* *C. braunii*
2	Chara Haven	pool	sand	*Naias*	30	45	9	9.4	1.3	*C. delicatula*
3	Chara Pond	cove	muck	*Carex* *Scirpus*	32	300	0	8.4	10.5	*C. canescens* *C. delicatula*
4	Cranberry Ditch	stream	sand-muck	*Callitriche* *Potamogeton*	18	12	0	5.9	0.0	*N. flexilis*
5	Dam Pond	dammed stream	sand-muck	*Typha* *Scirpus*	25	19	0	6.7	1.7 0.0	—
6	Endicott Pond (93)	kettle	muck	*Nymphaea* *Nuphar*	25	31	0	7.2	0.0	—
7	Flax Pond (30)	kettle	rock-muck	*Nymphaea* *Myriophyllum*	24	2	0	4.3 4.8	0.0	—
8	Fresh Pond (96)	deep pond	pebble	none	26	7	0	6.9 5.9	0.0	—
9	Great Pond	cove	muck	—	—	263	0	8.2	31.5	—
10	Green Pond	cove	sand	*Ruppia* *Zostera*	—	186	0	8.2	15.6	—
11	Harper Pond	shallow kettle	muck	*Potamogeton* *Proserpinaca*	29 25	10	0	5.7 5.6	0.0	*N. morongii*
12	Jones Pond (31)	deep lake	muck	*Nymphaea* *Utricularia*	29 25	9 6	0 0	6.3 5.8	0.0 0.0	—
13	Little Pond	cove	sand	*Nymphaea* *Potamogeton*	30	32 47	0 7	9.5	1.25 1.12	*C. braunii* *C. delicatula*
14	Ice House Pond (25)	deep lake	sand-rock	*Nymphaea* *Myriophyllum* *Utricularia*	—	0	0	—	0.0	—

TABLE I—*Continued*

	Habitat	Basin type	Bottom type	Plants	Temp. °C	Alkalinity		pH	NaCl	Characeae
						M.O. ppm	ph-th ppm		0/00*	(*C* = *Chara*, *N* = *Nitella*)
15	Morse Pond	pond	sand-muck	*Pontederia* *Utricularia* *Decadon* *Potamogeton*	27	12	0	6.9	0.0	*N. transilis* *N. megacarpa*
16	Nobksa Pond (1)	cove	sand-muck	*Potamogeton* *Myriophyllum*	23.8	25	0	9.2	1.73	*C. braunii* (1 spec., 1949)
17	Oyster Pond (20)	cove	sand-rock	*Potamogeton*	22	59	8	7.2	1.42 0.34	*C. braunii* *C. delicatula*
18	Salt Pond (19)	cove	sand-rock	*Potamogeton*	34	45	18	—	9.52 3.30	*C. delicatula* *C. braunii* *C. canescens*
19	Sandwich Pond	deep pond	sand-muck	—	—	53	16	—	1.01	*C. braunii*
20	Shiverick Pond	deep pond	sand-muck	*Decadon*	24 26	45	9	7.7 9.4	0.0 0.1	—
21	Sols Pond	deep pond	sand-muck	*Gratiola* *Decadon* *Pontederia*	29	77	11	9.2	0.0	—
22	Weeks Pond	deep pond	clay-muck	*Nymphaea* *Potamogeton*	27 29	20 19	9 0	7.1 6.7	0.0 0.0	*N. flexilis* *N. megacarpa* *N. transilis* *C. braunii*
23	Whittemore Pond	kettle	muck-rock	*Myriophyllum*	22 33	—	—	4.45 4.05	0.0	—
24	Whittemore Estate Pond	pond	muck	*Fontinalis* *Myriophyllum*	31.5	4	0	4.9	0.0	—
25	Wood Pond	pool	muck	none	22	52	0	6.6	0.0	—
26	Coona-messet River	stream	sand-muck	*Callitriche* *Potamogeton*	18	19 15	0	6.6	0.0	*N. flexilis*

* 0/00 = parts per thousand.

Characeae found. In addition, the pH values were determined with a Beckman Model G glass electrode pH meter. The determinations were run in the field on samples taken directly from the water. Salinity determinations were made in $^0/_{00}$ (= parts per thousand) by a simplification of the Knudsen method as outlined for use by the Oceanographic Institute, Woods Hole; and were standardized against standard sea water (Cl = 19.37 $^0/_{00}$) obtained from that institution. Methyl orange alkalinity (abbreviated as "M.O.") and Phenolphthalein alkalinity (abbreviated as "ph-th") were determined by the titrimetric methods outlined in the "Standard Methods of Water Analysis" (Amer. Publ. Health Assoc. 1946). Temperatures at depths of 3–6 inches were obtained by an ordinary chemical thermometer. Samples for such determinations, with the exceptions of pH and temperature, were collected in glass stoppered bottles, and analyses were run within three hours after collections. The survey was run during periods of warm, clear weather during the months of July and August.

A taxonomic study of the species of Characeae collected was made concurrently, and the results of this work have been reported elsewhere (Wood 1949). That work provides the

taxonomic background for the present study, and can be consulted for discussion of the various forms.

Data

The field notes, observations, analyses, and species of Characeae found are listed in Table I. The names of the water systems follow those used by Croasdale (1935) and Wood (1949).

The data contained in Table I were rearranged in accordance with increasing intensities of each measurable factor, or were entered against descriptive terms in cases of basin type or bottom type, or against species of associated plants in Table II.

A study of the table reveals that little or no correlation is indicated between species occurrence and temperature, ph-th alkalinity, or bottom type. On the other hand, a marked correlation is indicated between species occurrence and salinity, M.O. alkalinity, and pH values. The type of basin shows a fair degree of correlation with species occurrence.

Summary

1. A survey of twenty-six water systems in the Woods Hole region, Massachusetts, was made to determine the occurrence of Characeae with respect to major environmental conditions.

2. The factors considered included type of

Table II. *Species of Characeae, Chara (C) and Nitella (N), and their occurrence correlated with the intensity of certain environmental factors; the habitat numbers refer to those at the left in Table I*

Factor	Habitats	*N. flexilis*	*N. megacarpa*	*N. transitis*	*N. morongii*	*C. braunii*	*C. delicatula*	*C. canescens*	Number of habitats	Number of habitats with Characeae
Basin Type										
Cove	3, 9, 10, 13, 16, 17, 18	0	0	0	0	3	4	3	7	5
Pond	8, 15, 19, 20, 21, 22, 24	1	2	2	0	2	0	0	7	3
Pool	2, 25	0	0	0	0	1	1	0	2	1
Stream	4, 26	2	0	0	0	0	0	0	2	1
Kettle	6, 7, 11, 23	0	0	0	1	0	0	0	4	1
Lake	1, 12, 14	1	1	1	0	0	0	0	3	1
Dammed stream	5	0	0	0	0	0	0	0	1	0
Bottom Type										
Sand	1, 2, 10, 13	1	1	1	0	2	2	0	4	3
Sand-muck	4, 5, 15, 16, 20, 21, 26	2	1	1	0	1	0	0	7	3
Clay	22	1	1	1	0	1	0	0	1	1
Muck	3, 6, 7, 9, 11, 12, 24, 25	0	0	1	0	0	0	0	8	1
Cobble	8, 14, 17, 18, 23	0	0	0	0	2	3	2	5	2
Plants										
Callitriche	4, 26	1	0	0	0	0	0	0	2	2
Carex	3	0	0	0	0	0	1	1	1	1
Decadon	15, 21	0	1	1	0	0	0	0	2	1
Fontinalis	19, 24	0	0	0	0	1	0	0	2	1
Gratiola	21	0	0	0	0	0	0	0	1	0
Lobelia	1	1	1	1	0	0	0	0	1	1
Myriophyllum	7, 14, 16, 23, 24	0	0	0	0	1	0	0	5	1
Naias	2	0	0	0	0	1	1	0	1	1
Nuphar	6	0	0	0	0	0	0	0	1	0
Nymphaea	6, 7, 12, 13, 14, 22	1	1	1	0	2	1	0	6	2
Pontederia	15, 21	0	1	1	0	0	0	0	2	1
Potamogeton	4, 11, 13, 15, 16, 22	2	2	2	1	3	1	0	6	6
Ruppia	10	0	0	0	0	0	0	0	1	0
Scirpus	3, 5	0	0	0	0	0	1	1	2	1
Typha	5	0	0	0	0	0	0	0	1	0
Utricularia	12, 14, 15	0	1	1	0	0	0	0	3	1
Zostera	10	0	0	0	0	0	0	0	1	0

TABLE II—*Continued*

Factor	Habitats	*N. flexilis*	*N. megacarpa*	*N. transitis*	*N. morongii*	*C. brauinii*	*C. delicatula*	*C. canescens*	Number of habitats	Number of habitats with Characeae
Temperature										
17–20	4, 26	2	0	0	0	0	0	0	2	2
21–22	17, 25	0	0	0	0	1	1	0	2	1
23–25	1, 5, 6, 7, 8, 16, 20	1	1	1	0	1	0	0	7	2
26–28	11, 12, 22	1	1	1	1	1	0	0	3	2
29–	2, 3, 13, 15, 18, 21, 23, 24	0	1	1	0	3	4	2	8	5
M.O. Alkalinity										
0–10	7, 8, 11, 12, 14, 24, 26	1	0	0	1	0	0	0	8	2
11–20	1, 4, 5, 15, 22	3	3	2	0	1	0	0	5	3
21–30	16	0	0	0	0	1	0	0	1	1
31–40	6, 13	0	0	0	0	1	1	0	2	1
41–50	2, 18, 19, 20, 25	0	0	0	0	3	2	1	5	3
51–100	17, 21	0	0	0	0	1	1	0	2	1
101–	3, 9, 10	0	0	0	0	0	1	1	3	1
Ph-Th Alkalinity										
0–7	1, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 24, 25, 26	3	2	2	1	2	2	1	18	8
8–14	2, 17, 20, 21	0	0	0	0	2	2	0	4	2
15–21	18, 19, 22	1	1	1	0	3	1	1	3	2
pH Values										
4–5	7, 23, 24	0	0	0	0	0	0	0	3	0
5–6	4, 11	1	0	0	1	0	0	0	2	2
6–7	1, 5, 8, 12, 15, 22, 25, 26	3	3	3	0	0	1	0	7	4
7–8	6, 17	0	0	0	0	1	1	0	2	1
8–9	2, 3, 9, 10, 13, 16, 20, 21	0	0	0	0	2	4	1	8	3
Salinity										
0.0	1, 4, 5, 6, 7, 8, 11, 12, 14, 15, 21, 22, 23, 24, 25, 26	3	3	3	1	1	0	0	16	4
0.1– 2.0	2, 13, 16, 17, 19, 20	0	0	0	0	5	3	0	6	4
2.1– 5.0		0	0	0	0	0	0	0	0	0
5.1–10	18	0	0	0	0	1	1	1	1	1
10.1–15.0	3	0	0	0	0	0	1	1	1	1
15.1–30	9, 10	0	0	0	0	0	0	0	2	0

water basin, bottom, associated plants, pH, salinity, methyl orange (M.O.) and ph-th alkalinity, and temperature.

3. Of the factors considered, marked correlation was found between species occurrence and salinity, M.O. alkalinity, and pH values. A fair correlation was found with type of basin. Little or no correlation was found for temperature, ph-th alkalinity, or type of bottom.

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SOME ENVIRONMENTAL CONDITIONS INFLUENCING LIFE AT HIGH ALTITUDES

In the accompanying figure (Fig. 1) an attempt has been made to illustrate graphically two features of the high altitude environment on Mt. Orizaba in Mexico. These are (1) the reduced significance of air temperature as a measure of the temperature of the environment, and (2) the somewhat paradoxical situation in which animals of the same habitat may be active either in an arctic climate or in a tropical desert environment.

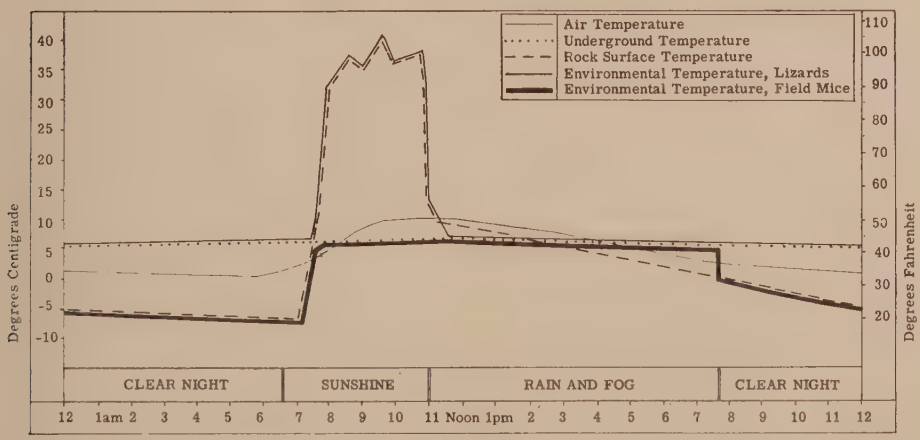

Fig. 1. A typical July day at 4,120 meters on Mt. Orizaba, Mexico.

The commonest lizard of high altitudes in Mexico, *Sceloporus microlepidotus*, ranges from low elevations to an observed 4,500 meters (14,800 feet) on Mt. Orizaba. The activity of these lizards at elevations above tree line (4,120 meters) is almost totally confined to periods of sunshine, as the air temperature at these altitudes rarely exceeds 10° C. They appear shortly after sunrise and, for a period of time before the rocks have warmed up, react dramatically to any passing cloud. Even a wisp of mist will send them scurrying for cover. After the exposed rocks have reached temperatures above 18° C., the lizards are much less sensitive to shade temperatures as they are able to flatten themselves out and absorb heat from the surface of the rocks. As indicated on the graph, sunshine is a rather brief event during the rainy season, but the usual three or four hours of warmth allow the lizards a sufficient length of time for hunting food. An analysis of the stomach contents of several lizards shows that a full stomach of about 35 assorted insects, chiefly Diptera and Hymenoptera, is acquired in approximately two hours. Food is abundant in the warm sunshine when most of the flying insects are active.

At night, and during the heavily overcast afternoons, the lizards remain dormant under loose rocks or in deep crevices. Their choice of shelter is fairly specific in that the rock under which they burrow is always over eight inches thick. At tree line they form large populations on the sunny eastern exposures of old lava flows; in an area measuring approximately 15 by 30 meters, a total of 42 lizards were counted under the rocks. Turning to the graph it can be seen that, for the greater part of the night and day, the lizards are underground in an environmental temperature that remains at about

5° C. For a few hours in the morning they are exceedingly active in a tropical desert heat ranging from 27° C. to 40.6° C. and usually above 35° C. Their environmental temperature is strikingly different from the air temperature as obtained by standard techniques.

The field mouse *Microtus mexicanus* is commonly seen at night running between the tall tufts of grass above tree line. The grass, which is the flowering plant reaching the highest altitude in North America, extends up to 4,640 meters (15,200 feet), and the mice may possibly live at that extreme elevation. During the rainy season on Mt. Orizaba, the nights are generally cloudless, and consequently there is a great deal of re-radiation of heat from the earth. Rock surface temperature readings at night differ from sheltered thermometer temperatures by as much as 8° C., such that here again standard air temperatures do not give an accurate measure of the actual temperature of the environment. Although the field mice may spend many of their active hours sheltered in the grass, they are nevertheless to be found in an arctic environment where freezing temperatures can be experienced every clear night of the year. During the day the mice sleep in the warmest sheltered nest they can find. Thus they occupy burrows beneath the same, or similar, rocks under which the lizards spend the coldest phase of their existence.

Gadow's salamander, *Pseudoeurycea gadovii*, which can be found under the rocks above tree line as well as in the soil under the highest trees, occupies a climatic category somewhat different from that of the lizards and mice. This amphibian, which holds the world altitude record for salamanders, seems to depend upon warmer evenings and overcast nights for its activity during the rainy season. It remains completely hidden during the hours of sunshine when the amount of evaporation must be extremely high. During two weeks of observation the salamanders were not seen to move from under the rocks. However, when stomach analyses were made on two specimens, it was found that one of the pair contained a single undigested grass spider. From this it would appear that the salamanders may to some extent be dependent upon various arthropods which climb under the rocks for shelter. It is interesting to note that in an area approximately 15 meters square, eight salamanders were discovered under the rocks. They were not found elsewhere in the locality, and it is possible that a small group of this sort is completely isolated from other members of the species.

The environmental temperatures of other high altitude animals may be inferred from the accompanying graph. Centipedes, worms, and various insects, such as the many Collembola, complete their life cycles at a temperature which does not vary much above or below 5° C. Birds are most active during the early morning hours of sunshine. The only birds commonly observed at tree line during the afternoon rain were towhees. At night the sheltered nests of birds would be exposed to temperatures similar to standard air temperature, which rarely drops below freezing at 4,120 meters (13,500 feet) in July. Humming birds at these heights, however, are subject to a unique variant of the high altitude environment. During the morning sunshine, individual humming birds can be seen visiting the bright patches of castilleja flowers at elevations up to 4,420 meters (14,500 feet). They are, however, merely high altitude transients and fly rapidly to lower altitudes upon the first indications of the late morning fog.

The use of the term "typical day" is not as indefinite as it may sound when applied to the climatic conditions on Mt. Orizaba during the rainy months. The conditions described in the accompanying graph would, with only minor differences, apply to all but three of 28 days. During the month of July 1949, there was but one day when the sun shone with regularity. On two occasions the sky was overcast and it rained during the night. On the same two occasions there was no sun in the morning. Variations of the "typical day" existed occasionally when there was a short period of sunshine following the afternoon rain. The time of onset of fog and rain was also erratic in that it occurred between 9:00 A.M. and 1:00 P.M., but most frequently between 10:00 A.M. and 11:00 A.M. as shown on the graph.

Shade air temperatures were obtained each day with a sheltered maximum-minimum thermometer. Night air temperatures usually dipped to 0° C. and then rose after sunrise to 10° C. before the fog set in, after which there was a gradual drop in temperature. A maximum of 15.6° C. and a minimum of −1.7° C. were recorded for the four weeks at 4,120 meters. Ground temperatures were obtained by placing a maximum-minimum thermometer under rocks where lizards had been found. In order to avoid damage to the thermometer, the instrument was placed in the sand beneath the rocks in a position resembling that assumed by the lizards. From seven readings, three of which extended over a 24-hour period, the temperature of the lizard burrows was found to vary between 4.4° C. and 7.2° C.

On two mornings, six experimental sun temperatures were obtained. A thermometer with a blackened bulb and a similar thermometer with a silver-colored bulb were together exposed to the sun. At 9:45 A.M., the last reading before intervening clouds terminated the test, a black bulb temperature of 46.5° C. and a silver bulb

temperature of 40.6° C. were recorded. These temperatures would suggest that the environmental temperatures of animals in the sun depend upon the color of the animal. However, as half of the animal is shaded, the true environmental temperature can only be estimated. Further information concerning the temperature of the environment in the sun was obtained from the subjective standpoint of a human observer. At 4,120 meters, when the air temperature was near 10° C., the sun was warm and excess clothing was discarded. There was a burning sensation on the bare skin, but one felt that the environment was at a temperature resembling that of a warm room rather than the 40.6° C. to 46.5° C. of the desert shade. There are no doubt many factors which influence the environmental temperature in the sun, and the simple use of thermometers may give an erroneous conclusion.

Temperatures of the rocks were obtained rather crudely. At first thermometers were held in place by the use of black friction tape and transparent Scotch tape. This method met with some success. However, higher and better sustained temperatures, less influenced by air temperature, were obtained by placing the bulb of the thermometer in a close fitting, shallow groove in the rock exposed at a right angle to the sun. Greater contact with the rock was accomplished by covering the bulb with thin chips of rock and large grains of sand. A total of 42 temperature readings were made in this manner. As might be expected, there was considerable difference in the recorded temperatures depending on the angle of exposure, the general coloration, and the length of time they had remained in full sunlight. Temperatures of the rocks at night were not obtained with consistency. One reading before dawn was −7.2° C. Other readings made shortly before 9:00 P.M. on five consecutive evenings were between −2° C. and −4°C. In the afternoons, when the rocks were usually wet with rain, surface temperatures fell slightly below air temperature.

All relative humidity readings taken in the shade among the trees at tree line were above 90 per cent during the month of July. Nevertheless, it should be considered that with the combination of low barometric pressure, high wind velocities, and high temperatures for rock and animal surfaces alike, evaporation in exposed areas must be intense. Thus, in the space of a few feet, there may be found conditions of nearly continual dampness suddenly merging into extreme aridity.

From the foregoing discussion it is evident that at high altitudes the differences between microclimates are exaggerated. A wide selection of temperatures is available to organisms capable of movement. The limiting temperatures for animals which do not readily survive freezing are to be found in easily accessible underground shelters. Thus animals and, to a lesser extent, plants can be classified into several climatic categories according to their temperature requirements. In broad outline these are as follows:

(1) Plants and perhaps some insects subject to the complete range of temperatures (approx. −7.2° C. to approx. 40.6° C.).

(2) Animals which are active only in the sunlight or on rocks heated by the sun, *e.g.*, lizards and flying insects (27° C. to 40.6°C.).

(3) Animals migrating to high altitudes during periods of sunshine, *e.g.*, humming birds.

(4) Animals exposed to shade air temperatures, *e.g.*, some birds and other animals of the tree line (0° C. to 10° C.)

(5) Animals continually subject to underground temperatures, *e.g.*, centipedes, worms, many insects (? 5° C. to 7° C.).

(6) Animals active during periods of cloudiness, *e.g.*, salamanders (0° C. to 7° C.).

(7) Animals active at night temperatures, *e.g.*, field mice (approx. −7.2° C. to 0° C.).

Summary

At an elevation of 4,120 meters (13,500 feet) on Mt. Orizaba, Mexico, the lizard, *Sceloporus microlepidotus,* is active only during brief periods of sunshine. The temperature of the environment where the lizards are active is usually above 35° C. Many flying insects also confine their activity to periods of sunshine, and the lizards are able to obtain adequate quantities of food even when sunshine is limited to two hours in the morning. The field mouse, *Microtus mexicanus,* is active at night. As the nights are cloudless, the temperature of the environment of the field mice may fall as low as −7.2° C. Both lizards and mice find shelter under the rocks (environmental temperature approximately 5° C.) during the afternoon rain and fog. However, the lizards are active in a tropical desert environment, while the field mice exist in an arctic climate. Furthermore, the temperatures to which these animals are exposed do not coincide with the temperature of the air.

Salamanders generally remain beneath the rocks where they may be partially dependent upon transient arthropods for food. The environmental temperatures of various other high altitude animals have been inferred from their habits, and it has been possible to distinguish seven groups of high altitude organisms according to their temperature preferences.

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PHYTOSOCIOLOGICAL ANALYSIS OF A TALL-GRASS PRAIRIE IN MARSHALL COUNTY, OKLAHOMA

Introduction

Bruner (1931), in his description of the true tall-grass prairie of Oklahoma, indicated that the dominant plant was little bluestem (*Andropogon scoparius*). He pointed out, however, that it was usually associated with big bluestem (*Andropogon gerardi*), switch grass (*Panicum virgatum*), and Indian grass (*Sorghastrum nutans*), or with elements from the mixed prairie and short-grass plains. P. L. Welch [1] reported that little bluestem was the dominant plant of the tall-grass prairie of McClain County, Oklahoma. F. R. Nease [2] pointed out that the original tall-grass prairie in south central Oklahoma (west of the area studied in the present investigation) was dominated by little bluestem in the drier portions whereas switch grass, sand bluestem (*Andropogon hallii* Hack.), and Indian grass were more important in the moister areas. R. W. Kelting [3] found that the dominant species in a virgin tall-grass prairie plot in Cleveland County, Oklahoma, were little bluestem, big bluestem, switch grass, Indian grass and prairie aster (*Aster ericoides*).

In July, 1950, a project was undertaken to determine (1) the composition of a tall-grass prairie community in southern Oklahoma, and (2) what constitutes adequate sampling of a tall-grass prairie community. The prairie plot under consideration was located about ten miles

Table I. *Comparison of average* areal covers and frequencies of species in prairie plot based on 20 vs. 40 quadrats. Species arranged according to decreasing cover (based on 40 quadrats)*

Species	20 Quadrats		40 Quadrats	
	Cover (%)	Frequency (%)	Cover (%)	Frequency (%)
1. *Sorghastrum nutans* (L.) Nash	8	70	8	78
2. *Panicum virgatum* L.	6	85	4	68
3. *Andropogon gerardi* Vitman	4	35	3	48
4. *Silphium laciniatum* L.	2	10	3	18
5. *Desmanthus illinoensis* (Michx.) MacM.	2	55	2	58
6. *Bouteloua curtipendula* (Michx.) Torr.	2	60	2	50
7. *Andropogon scoparius* Michx.	0.2	25	2	30
8. *Helianthus maximiliana* Schrad.	2	25	2	28
9. *Schrankia nuttallii* (DC.) Standl.	1	30	2—	35
10. *Ruellia humilis* Nutt. var.	1	50	1	45
11. *Solidago* sp.	1	20	1	22
12. *Sporobolus asper* (Michx.) Kunth	0.6	40	0.9	42
13. *Tragia urticifolia* Michx.	1	60	0.8	50
14. *Houstonia nigricans* (Lam.) Fern.	0.4	40	0.5	42
15. *Krameria lanceolata* Torr.	0	0	0.3	5
16. *Carex* sp.	0.1	35	0.2	40
17. *Aster ericoides* L.	0.1	10	0.2	15
18. *Penstemon* sp.	0.4	10	0.2	5
19. *Dyssodia tagetoides* T. & G.	0.2	5	0.2	5
20. *Liatris squarrosa* (L.) Michx.	trace#	10	0.1	12
21. *Phyllanthus polygonoides* Nutt.	trace	5	0.1	8
22. *Sporobolus cryptandrus* (Torr.) Gray	0.2	15	0.1	8
23. *Rosa setigera* Michx.	0.2	5	0.1	5
24. *Eleocharis* sp.	0.2	5	0.1	2
25. *Eriogonum longifolium* Nutt.	0.2	5	0.1	2
26. *Neptunia lutea* (Leavenw.) Benth.	0.2	5	0.1	2
27. *Petalostemum purpureum* (Vent.) Rydb.	0.1	15	trace	15
28. *Evolvulus pilosus* Nutt.	trace	5	trace	10
29. *Bifora americana* (DC.) S. Wats.	trace	5	trace	8

* All numbers over one rounded off to nearest whole number.
# "Trace" refers to any average cover less than 0.1%.

[1] A reconnaissance of a typical Oklahoma prairie. Unpublished thesis, Univ. of Oklahoma. 1929.

[2] Range deterioration in south central Oklahoma. Unpublished thesis, Univ. of Oklahoma.

[3] Vegetation and soil conditions of prairie and pasture plots in central Oklahoma. Unpublished thesis, Univ. of Oklahoma.

north of Willis, Oklahoma, in Section 29, Township 6 S., Range 5 E. The plot, which was on a gentle west-facing slope, had been mowed several times for hay but, according to available information, had never been grazed or plowed.

Methods

The study was conducted as a plant ecology class project at the University of Oklahoma Biological Station. For purposes of the investigation, the class was divided into two teams, each team analyzing quadrats on one half of the plot only. The analysis consisted of determining and recording the areal cover of the living material of each species present (expressed in per cent of quadrat area), and the total cover afforded by both dead and living material. Based on previous experience of the author and other workers (Penfound 1945, Raunkiaer 1909), square quadrat frames encompassing 0.1 square meter areas were used to facilitate the estimation of areal cover and to increase the accuracy of the frequency data obtained. In addition, two area gauges were available for each team, one representing 1% of the total quadrat area and the other representing 5% of that area.

The plot analyzed was in the shape of a rectangle, 180 by 750 feet in size. Quadrats were spaced about 60 feet apart along four parallel lines running lengthwise through the plot. The lines were spaced about 40 feet apart with each outside line being about 30 feet from the lateral margin of the plot. Ten quadrats were taken by each team on the first visit to the area. Four days later each team analyzed ten more quadrats in the same half of the plot as on the previous visit. The average cover and frequency percentages were then calculated for each half separately (on the basis of ten and twenty quadrats), and for the entire plot (on the basis of twenty and forty quadrats). Only the results for the entire plot based on twenty versus forty quadrats will be presented.

Results and Discussion

Characteristic species of the present prairie were delineated fairly well on the basis of twenty or forty quadrats. On the basis of average cover (Table I), the relative orders of species as determined by twenty versus forty quadrats were the same with the exception of seven species. Of these seven species, all except one had an average cover of less than 1% based

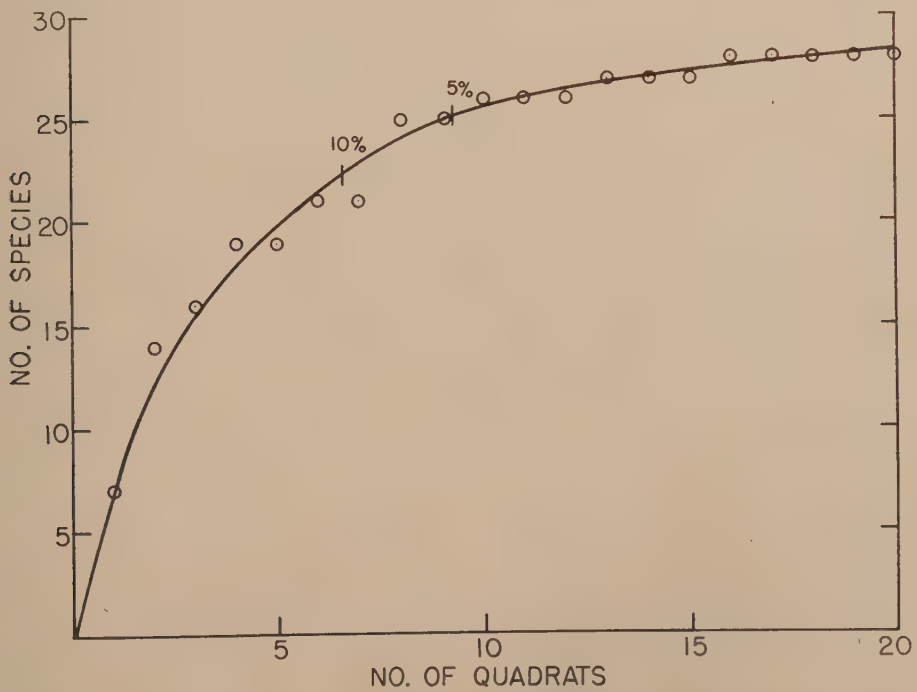

Fig. 1. Species-area curve for east half of tall-grass prairie plot. The 10% line on the curve indicates point where an increase of 10% in area gives a 10% increase in number of species. The 5% line indicates point where an increase of 10% in area gives a 5% increase in number of species.

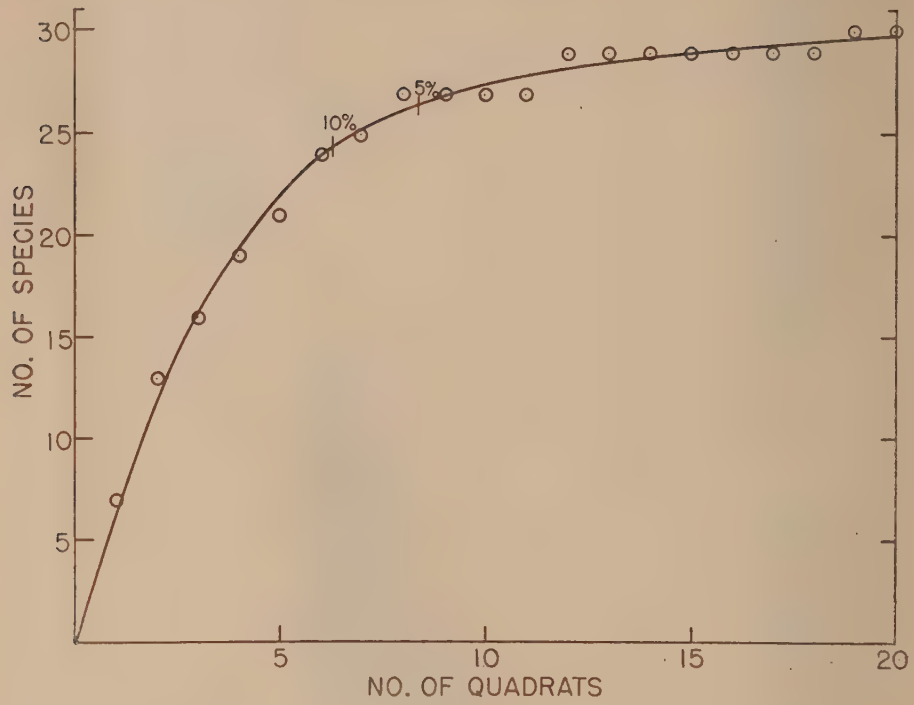

FIG. 2. Species-area curve for west half of prairie plot. Symbols same as for Figure 1.

on forty quadrats. Frequencies of most species were quite close on the basis of twenty versus forty quadrats.

The total area sampled in this investigation (forty 0.1 sq. m. quadrats) represented only about 0.032% of the area in the prairie plot. This appears to be an extremely small sample. Using the method suggested by Cain (1938) for determining the break in the species-area curve, however, it was found that this break (point where a 10% increase in area gives a 10% increase in species) occurred after slightly less than seven quadrats on the east half of the plot (Fig. 1) and after slightly over six quadrats on the west half (Fig. 2). If one uses the point on the species-area curve (point where a 10% increase in area gives a 5% increase in species) which Cain (1938) considered to be a very conservative estimate of minimal area required for the determination of the characteristic species of a community, the break is found to occur after slightly over nine quadrats on the east half of the present plot and after about eight and one-half quadrats on the west half. The information obtained from the species-area curves and from Table I both suggest that even twenty quadrats of the size used would have been sufficient for the sampling of the present prairie area. In an analysis of six prairie stands on the Hempstead Plains, Long Island, New York, Cain (1937) found that a sample amounting to only 0.006% of the total area of the stands was sufficient to differentiate the characteristic species. In one instance (Mitchell Field), Cain sampled only 0.002% of the stand. Calculations based on data given by Albertson (1937) show that the sample used by him in an analysis of the big bluestem consociation of a 160 acre mixed prairie near Hays, Kansas, amounted to only 0.018% of the total area of the consociation. Most papers concerned with the analysis of prairie vegetation do not indicate what percentage of the total area was sampled nor do they give sufficient data to allow such a calculation. The prairie sampled in the present investigation was fairly homogeneous; this, of course, results in a sampling of a fairly high percentage of species in a few quadrats. Certainly the present sample area may not have been adequate if the community involved had been extremely heterogeneous.

It should be pointed out that the present sampling was probably inadequate to secure figures on cover and frequency which could be reproduced exactly by another group using similar methods. This is strongly suggested by the fact that the actual figures for cover and frequency varied somewhat on the basis

of twenty versus forty quadrats although the relative orders of the species stayed essentially the same (Table I). To obtain such exact figures would probably require a number of quadrats several times that required for a break in the species area curve as defined by Cain and as used in this paper. Penfound (1945) suggested a number of quadrats at least ten times that required for the break in the species-area curve as a proper *quantitative* sample in community analysis. Present data are insufficient either to substantiate or to disprove this suggestion.

In the present prairie a total of thirty-nine species was encountered, twenty-nine in the quadrats and ten additional species by careful reconnaissance (Tables I and II). Of this number probably only three species should be considered as dominants: *Sorghastrum nutans, Panicum virgatum,* and *Andropogon gerardi.* It is especially interesting to note here that *Andropogon scoparius,* which has been considered by most authors (Bruner 1931, Kelting,[3] Nease,[2] and Welch [1]) to be an important dominant in the tall-grass prairie of Oklahoma, has a relatively low frequency in the present prairie. As usual when intercepted by a quadrat, it covers a fairly large area thus making it appear fairly important on the basis of average cover alone.

A careful reconnaissance of many prairie areas throughout the southern half of Marshall County indicated that little bluestem is relatively unimportant as compared with the dominants mentioned previously. The prevalence, even on level upland prairie areas, of such species as switch grass, Indian grass, and big bluestem which are ordinarily found in slight depressions or moist slopes throughout most of the tall-grass prairie in Oklahoma is no doubt due to the fairly high rainfall. The annual precipitation over a 54-year period has averaged around 38 inches throughout Marshall County. This is a transition region between blackjack-post oak forest and the tall-grass prairie. The prairie occurs only on soils developed from limestones or clays whereas the forest occurs on all sandy soils.

Bruner reported that *Andropogon saccharoides* (silvery beard-grass) was an important dominant in the true prairie of Oklahoma, particularly in the southern part. The present study was, of course, made in the extreme southern part of the state and silvery beard-grass was not encountered in the plot which was analyzed. The present author, however, has never seen this species in any area which has not been pretty seriously disturbed.

TABLE II. *List of species from prairie plot not encountered in quadrats*

1. *Asclepias viridiflora* Raf.
2. *Croton texensis* (Klotzsch) Muell. Arg.
3. *Eryngium leavenworthii* T. & G.
4. *Heliotropium tenellum* (Nutt.) Torr.
5. *Ipomea* sp.
6. *Monarda dispersa* Small
7. *Onosmodium occidentale* Mackenz.
8. *Psoralea digitata* Nutt.
9. *Teucrium canadense* var. *virginicum* (L.) Eaton
10. *Verbena bipinnatifida* Nutt.

SUMMARY

1. Characteristic species of the tall grass prairie community studied were delineated fairly well on the basis of either twenty or forty 0.1 square meter quadrats. The actual figures for cover and frequency differed somewhat for most species on the basis of twenty versus forty quadrats, however. This was true despite the fact that the break in the species-area curve (point where a 10% increase in area gives a 10% increase in species) occurred after slightly less than seven quadrats on one-half of the plot and after slightly over six quadrats on the other half. Present data suggest, therefore, that several times the number of quadrats required for the break in the species-area curve would be needed to obtain exact reproducible data on cover and frequency.

2. A total of thirty-nine species was found in the prairie community. Of these, *Sorghastrum nutans, Panicum virgatum,* and *Andropogon gerardi* were considered the dominants. *Andropogon scoparius,* which is usually considered the most important dominant in the tall-grass prairie of Oklahoma, was considerably less important than the above species in the community studied. Careful reconnaissance of many prairie areas in southern Marshall County indicated that *Andropogon scoparius* is of considerably less significance throughout the area than are the dominants listed above.

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THE CALCULUS AND THE INOPERABLE EXPRESSION

When one studies the Calculus one is introduced to certain symbols—especially:

$$\frac{df(x)}{dx} \quad \text{and} \quad \int_{x_1}^{x_2} f(x)dx.$$

These symbols refer to mathematical operations which, *when performed*, reveal new relationships between the variables embodied in the equations. For the performance of such operations variables must be expressed in the form of equations which can be differentiated or integrated. If the variables cannot be expressed in the form of operable equations then use of the Calculus symbols adds little to our knowledge of the relationships between the variables.

For example, the plankton of Lake Erie varies from time to time and at any given time it varies from place to place. I can rewrite the above sentence using the Calculus notation as follows: (let P represent plankton, t represent time and x represent distance in any direction from Put-In-Bay)

$$\frac{dP}{dt} = f(t) \quad \text{and} \quad \frac{dP}{dx} = f(x).$$

This means that the rate of change of plankton with respect to time is a function of time and the rate of change of plankton with respect to distance from Put-In-Bay is a function of the distance from Put-In-Bay. I could also state without fear of successful contradiction that

$$P = \int_{t_1}^{t_2} f(t)dt \quad \text{and} \quad P = \int_{x_1}^{x_2} f(x)dx,$$

where x_1 is Put-In-Bay and x_2 is somewhere else (within Lake Erie, a "boundary condition"). This means that the plankton accruing or decaying between two definite points of time is evaluated by the definite integral of the function of time between the limits under consideration, and the total plankton between Put-In-Bay and some other spot in the lake is evaluated by the definite integral of the function of distance between the limits indicated.

However, using the Calculus symbols in this way does not advance our knowledge of the relationship between plankton and time or space. Such use of the symbols can then serve only minor purposes, such as:

(1) The symbols can represent a sort of shorthand for the words "rate of change" or "sum of increments between. . . ." Such usage is not particularly advisable since it is usually necessary to write the words too for the benefit of the readers who are unfamiliar with this shorthand notation; hence, no space is saved and an unnecessary load is placed on the typesetter.

(2) It may be that someone some day will determine the $f(t)$ or the $f(x)$ and will be inspired to perform the indicated operations. But it seems likely that the researcher who determines the form of these functions will be able to set up the indicated differential equations himself.

(3) The presence of such symbols in the literature of aquatic ecology will warn the reader (the young one, at least) that he must study the Calculus if he intends to become a well-trained ecologist. He will be a bit disappointed if, after mastering the Calculus, he rereads the paper which inspired him and detects the trivial use made of this elegant tool.

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GAS EXCHANGE OF CYPRESS KNEES[1]

Introduction

One of the characteristic features of cypress (*Taxodium distichum* (L.) L. C. Rich.) swamps is the occurrence of the structures known as knees. These are vertical outgrowths from lateral roots which develop into somewhat conical structures, varying from a few inches to several feet in height. Although the knees arise from roots, they are not branch roots in the usual sense of the word because they are not produced by primary growth of a terminal meristem or root tip. For some unexplained reason the cambium becomes abnormally active in very localized areas on the upper surface of roots. The extraordinarily thick layers of xylem laid down in a very limited area each year soon produce the protuberances which are termed knees. Their development has been described by Hoffman (1927), and a diagram of a longitudinal section is shown in Figure 1.

According to Kurz and Demaree (1934) cypress knees do not develop in deep water, but only where the soil is alternately flooded and exposed, and they grow to a height about equal to the average high water level of their habitat. Beaven and Oosting (1939) reported a similar correlation between water level and height of knees, and Penfound (1934) stated that cypress knees do not develop where the period of flooding is very short or where the soil is almost continuously flooded.

Cypress knees, like other so-called pneumatophores, have frequently been regarded as aerating organs through which gas exchange with submerged roots occurs. Betts (1943), for example, after mentioning the occurrence of cypress knees, states, "These growths appear to serve the double purpose of anchorage and of organs to supply an increased amount of oxygen to the roots." Although similar statements have been made in various texts and semi-popular papers, little experimental evidence on the subject is available.

Schimper (1903) stated that the pneumatophores of *Bruguiera eriopetala* released such large amounts of carbon dioxide that it could scarcely have been produced by the pneumatophores themselves and must have come from the roots. Wells (1932) stated that if a cypress knee is inclosed in a container the oxygen concentration inside the container will decrease and the carbon dioxide concentration will increase. This statement is based on five measurements made on inclosed knees in 1925 by Dr. G. W. Goldsmith. The data from these determinations were never published.

Since no extensive data on gas exchange could be located, experiments were planned to obtain measurements in a twenty-year-old cypress plantation on the Duke Forest, in North Carolina. This plantation is on low land which is flooded intermittently by a stream. Numerous knees occur, ranging in size from mere protuberances to those a foot or more in height and eight to ten inches in diameter at the base. The general appearance of the swamp and the method of inclosing knees is shown in Figure 2.

Methods

A group of eight medium-sized knees was selected and inclosed in air-tight containers. In order to accomplish this, platforms were anchored on short posts just above the soil or water surface, with the knees projecting through holes cut in the center of the platforms. The space between the knee and the platform was sealed with a paraffin-beeswax mixture. Each knee was covered with a five-quart oil can provided with ¼ in. inlet and outlet tubes. The cans were anchored to the platforms with wire, and air-tight seals were made by pouring melted wax around their bases. The inlet and outlet tubes were kept closed, one with a piece of rubber tubing and clamp, the other by tying a small balloon over it (see Figure 2). The

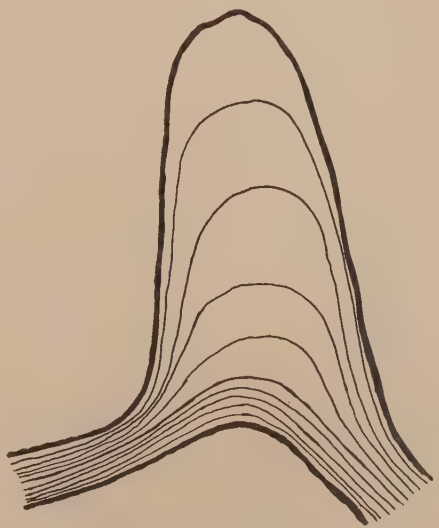

Fig. 1. Diagram of longitudinal section through a cypress knee. Note that it is produced by abnormal cambial activity on the upper side of the root which adds thick layers of wood each year.

[1] This investigation was partly financed by a grant from the Research Council of Duke University. The writers wish to acknowledge the assistance of Mr. Herman H. Wiebe in this project.

FIG. 2. General view of swamp and of two knees inclosed in metal containers. The balloon attached to the inlet tube of the can in the foreground provides for changes in gas volume resulting from changes in temperature.

balloon provided for expansion and contraction of the inclosed air with change in temperature and prevented development of large pressure differences between the air inside and outside of the can which might have caused leakage. Approximately one-third of the total volume of each knee was inclosed.

The oxygen concentration of the air within the cans was determined with a small portable Beckman oxygen analyzer. The oxygen analyzer was connected between the inlet and outlet of the can by small bore rubber tubing, and the air was circulated through it by means of a rubber bulb equipped with check valves. Before making an analysis the air in each can was stirred and mixed by repeated strokes of the rubber bulb. After sampling, the air in the cans was replaced with outside air by use of a tire pump. The gas was analyzed each morning in the principal series of measurements, each morning and afternoon in a short series of measurements made later in the summer.

Heavy rains occurred at the time the apparatus was being installed. As a result the soil was always saturated, and much of the time it was partly flooded. The water table had fallen somewhat at the time of the October measurements.

After sufficient preliminary measurements to develop a satisfactory technique the oxygen consumption of eight healthy knees was measured on August 5 and each morning thereafter for six days, except once, when a period of forty-eight hours elapsed between measurements. Four of the knees were then sawed loose from the roots on which they had developed and were left standing completely detached but in their original positions. The cut surfaces were below the surface of the mud and water. The gas in the containers inclosing both attached and detached knees was analyzed daily for oxygen for the next nine days and at intervals for another seven days. Results from this series of measurements are shown graphically in Figure 3.

Measurements of oxygen consumption and carbon dioxide production were made on the four knees which remained attached to the root systems. After determining the oxygen concentration of the air in each container, samples were removed in 30 ml. hypodermic syringes and carried to the laboratory, where the carbon dioxide concentration was determined in a Haldane-type gas analyzer. Duplicate determinations were made, and the averages were used. After measurements were made for five days, two of the knees were detached from the roots; and the other two were left as controls.

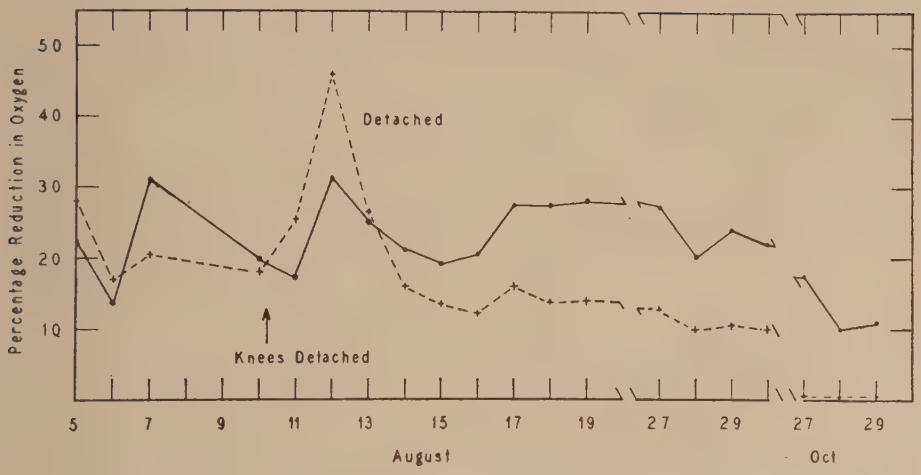

FIG. 3. Graphs showing oxygen consumption of attached and detached cypress knees. The experiment was started with eight knees of which four were detached on August 10. Only two knees remained attached in October.

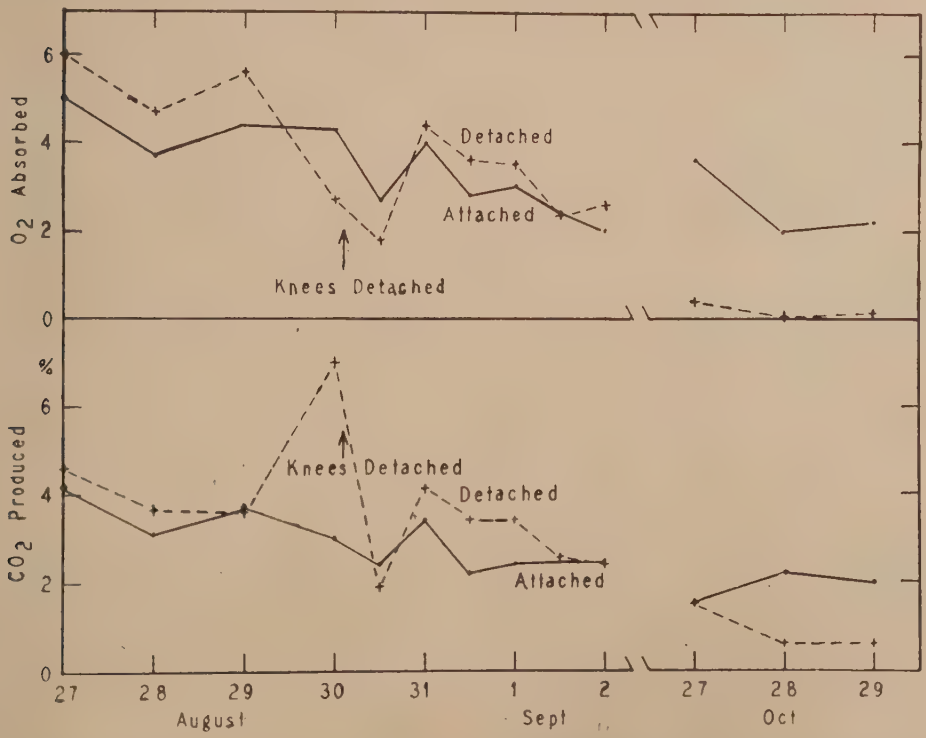

FIG. 4. Graphs showing oxygen consumption and carbon dioxide production of attached and detached knees, expressed as percentages of total gas content of containers. The experiment was started with four knees of which two were detached on August 30, leaving two attached knees for the September and October measurements.

The gas in the containers was then sampled each morning about 9 A.M. and each evening about 7 P.M. for the next three days. The results are summarized in Figure 4.

All of the knees were left standing until late in October when measurements of oxygen consumption and carbon dioxide production were made for three consecutive days. The results of these measurements are summarized in Figure 4. The experiment was terminated at this time, and the six detached knees were removed to the laboratory.

Discussion

It seems that if any considerable amount of oxygen transfer occurs through the knees to the root system, then when the knees are detached the amount of oxygen absorbed ought to be greatly reduced. The data presented in Figure 3 show the opposite behavior. The knees were detached between 9 and 10 A.M. and the containers immediately resealed. During the next two days more oxygen was used by the detached knees than by the attached knees. Perhaps this was the result of wounding. On the third day the oxygen consumption of attached and detached knees was similar, but the oxygen consumption of the detached knees then gradually decreased and was about 20 per cent lower than that of the attached knees by August 30. In late October the oxygen consumption had fallen to a negligible value. Probably this decrease in oxygen consumption is the result of a gradual decrease in food supply and death of cells of the detached roots. The relatively high carbon dioxide production of the detached roots in October probably was the result of microbial activity in the moist tissue rather than of cypress tissue respiration.

According to unpublished observations of H. H. Wiebe, cypress knees are fairly permeable to gases, and some movement of gases between the knees and roots is possible. Nevertheless, it seems probable that most of the oxygen absorbed by cypress knees is used by the meristematic tissue of the knees. A knee grows much more rapidly than the root on which it develops and has a large surface of meristematic tissue which doubtless uses large amounts of oxygen compared to the more slowly growing roots. Consideration of the average oxygen consumption of these knees indicates that all of the oxygen removed from the containers could easily have been used in the inclosed portions of the knees. Four knees absorbed an average of 225 ml. of oxygen per knee per day from August 5 to 10. Assuming that these knees contained only 10 per cent of living tissue, oxygen absorption averaged 13.7 ml. of oxygen per gram of dry weight of living tissue in 24 hours. This is considerably lower than the rate of oxygen consumption given for active plant tissue in Meyer and Anderson (1939: 514). It certainly is not necessary to assume that any appreciable gas movement occurs from the knees to the roots to account for the oxygen absorbed by the knees in these experiments. In fact, since only about one-third of each knee was inclosed in a container in this experiment, it seems doubtful if the inclosed portion absorbed enough oxygen to maintain a very high rate of meristematic activity in the entire knee. Perhaps only the upper portion which is most exposed to the air receives enough oxygen for optimum growth, hence the more rapid growth of the upper part of a knee.

There is indirect evidence that even if gas exchange with the roots does occur through cypress knees it is not essential to survival and growth. Kurz and Demaree (1934) comment that it is difficult to reconcile the alleged role of knees as aerating structures with their absence from trees growing in deep water. According to Penfound (1934), an unpublished manuscript of the U. S. Forest Service indicated that removal of cypress knees had little effect on tree growth.

The available evidence indicates that cypress knees play no important role as aerating organs. In fact, it appears that cypress trees grow as well without knees as with them.

Summary

A study was made of the oxygen consumption and carbon dioxide production of cypress knees. Eight knees were inclosed in air-tight cans, and the oxygen content of the inclosed air was determined each morning with a Beckman oxygen analyzer. The knees reduced the oxygen content 20 to 30 per cent in 24 hours. After several days half the knees were detached from the roots. The oxygen consumption of the detached knees was higher than that of the control knees during the first three days but then fell below that of attached knees and after three months was down to practically zero.

Oxygen consumption and carbon dioxide production of a group of four knees was measured for a few days; then two of the knees were detached from their roots. Oxygen consumption and carbon dioxide production of the detached knees was higher than that of the attached knees during the first two days but decreased with time.

Cypress knees possess a relatively large amount of very active cambial tissue, and this probably uses most of the oxygen absorbed. It is concluded that little gas exchange occurs between knees and the root systems on which they occur, and there is no evidence that they play an essential role as aerating structures for the roots.

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A VARIATION IN THE DISTRIBUTION OF A SPIONID POLYCHAETE IN THE WOODS HOLE REGION[1]

The annelid, *Polydora ciliata,* is a cosmopolitan species, common at Woods Hole, and endocommensal on the shells of certain bivalve molluscs. It has been well described by Wilson (1928). It has recently been shown to be a frequent inhabitant in the Carolina oyster (Lunz 1941), the commercial value of which is reduced because the worm tubes crowd the mollusc and cause it to secrete extra nacre over the tubes and borings.

At Woods Hole this species was found living in the shells of the common scallop, *Pecten irradians.* The mud tubes of the worm are on the inside of the valve next to the scallop, but the latter covers these completely, so that the worm's opening to the outside is restricted to the margin of the shell; or the worm may bore a hole completely through the shell to the outside. The latter is the more frequent type in the shells studied. A mud-tube, through which the spionid extrudes its head and peristomial palps, extends about 2 to 3 mm. beyond the external opening in the shell. The valves of the scallops must be examined internally for the presence of black cases, and these structures must be broken and examined to ascertain the presence and identity of the worm.

Samples of scallops taken from two localities near Woods Hole tentatively indicated a difference in the frequency of occurrence of the *Polydora ciliata* in the two samples. Further studies were made and the results are shown in Table I. The difference between the two samples is highly significant.

North Falmouth is about six miles north of Woods Hole on Buzzards Bay, and Lagoon Pond is about seven miles south across Vineyard Sound on the island of Martha's Vineyard.

It is surprising to find such a difference in the frequency of affected scallops from these two localities. The temperature at both places was 24° C. and the salinities differed by only 9 parts per million, both within the normal salinity range. No major environmental differences were observed. It was shown (Lunz 1941) that the worm enters the oyster while the valves are open. It would seem most likely, then, that the spionid would settle on the lower shell. In the scallops examined the upper or left valve was the one most frequently affected. Since scallops usually rest on their right sides,

TABLE I. *Distribution of the endocommensal* Polydora ciliata *found in samples of* Pecten irradians *taken from two different localities near Woods Hole*

Location	No. of scallops examined	No. of affected scallops		
		Left valve	Right valve	Both valves
Lagoon Pond, Martha's Vineyard	82	38 46.3%	6 7.3%	7 8.5%
North Falmouth	50	4 8.0%	4 8.0%	2 4.0%

$\chi^2 = > 20$; N = 1; P = < .001.

[1] The writer is indebted to the Woods Hole Marine Biological Laboratory for making available the necessary facilities and supplies. He especially wishes to thank Marian H. Pettibone of the U. S. National Museum for her interest and cooperation in this investigation.

FIG. 1. Ectocommensal molluscs on scallops from two localities near Woods Hole, Mass. Those from North Falmouth, on the right, carry *Anomia simplex* while those from Lagoon Pond, on the left, carry *Crepidula fornicata*. Both localities yield scallops carrying common brown and red algae, but those from North Falmouth are more heavily incrusted. The algae together with the *Anomia* leave hardly a free spot on the shell.

the left shells would be most free of mud and sand which might obstruct the tube openings. These molluscs frequently swim about, however, and it is doubtful whether the right sides actually become deeply inbedded in the substratum. Why and how this polychaete selects the upper, left shell is itself an interesting problem.

One additional discrepancy was noted. The scallops from Lagoon Pond were covered with the small gastropod, *Crepidula fornicata*. Those from North Falmouth lacked this ectocommensal mollusc and carried instead the small pelecypod, *Anomia simplex* (Fig. 1). Both of these species, moreover, are cosmopolitan forms and why they should be so distributed raises another question. The following explanation is offered as a possible reason for the unequal distribution of the endocommensal *P. ciliata* in relation to the distribution of the ectocommensal molluscs.

The *Crepidula*, though rather sluggish in movement, can and do change position from time to time. This is exemplified by the fact that after the scallops containing them had remained in an aquarium for several hours most of the *Crepidula* were found attached to the glass sides of the aquarium. Such migrations were never found with *Anomia*. Rather, this animal projects a calcified byssus with which it fastens itself to the shell. Such dense populations of sessile forms cemented close together by so many byssuses may prevent the spionid from establishing or maintaining an external opening through either valve.

It is suggested, therefore, that the unequal distribution of *Polydora ciliata* may be the result of a form of competition. While some ecological differences probably play a part, they are not at present obvious.

The writer is aware, however, that while the figures reported above are quite significant, they represent single samples. The first samples in which this difference was indicated were not accurately tabulated, though the results were indicative. Further samples should be checked from each locality and a thorough study undertaken to determine the reasons for the differences described.

Summary

The spionid polychaete, *Polydora ciliata,* which lives endocommensally on the shells of scallops (*Pecten irradians*), occurs with significantly different frequencies in two localities in the Woods Hole, Mass. region. This is negatively correlated with the degree to which the scallops are covered externally by the shells of attached *Anomia,* but attached shells of *Crepidula* do not appear to affect the frequency of *Polydora* in the scallops.

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AN OUTLINE FOR ECOLOGICAL LIFE HISTORIES OF HERBACEOUS VASCULAR HYDROPHYTES

The present paper is one of a series of outlines of ecological life history studies appearing in Ecology, under the sponsorship of the Committee on Ecological Life Histories. The following outline concerns herbaceous vascular hydrophytes. These are plants that "grow in water, in soil covered with water, or in soil that is usually saturated" (Weaver and Clements 1938). According to the definition, hydrophytes would include both wetland and aquatic species. Among the wetland and aquatic types there are several carnivorous species whose life histories are described, in part, by Lloyd (1942). In view of the gradual transition from fresh water, through brackish water to salt water habitats, and the uninterrupted shift from fresh water to salt water species, it seems logical to include both glykophytes and halophytes in the present outline. Glykophytes and halophytes are found among the thallophytes, bryophytes, pteridophytes, and spermatophytes (Uphof 1941). However, herbaceous vascular hydrophytes occur only in the pteridophytes and spermatophytes. According to the more modern natural classification, herbaceous vascular hydrophytes occur in the following classes of the Phylum Tracheophyta: Lycopodineae, Equisitineae, Filicineae, and Angiospermae. On the basis of the position of their perennating buds, herbaceous vascular hydrophytes belong to the following life-form classes of Raunkiaer: therophytes, hydrophytes, geophytes, hemicryptophytes, and chamaephytes. Definitions and subdivisions of the above classes are given by Braun-Blanquet (1932) and Raunkiaer (1934).

Types of Herbaceous Hydrophytes

In the delineation of types of herbaceous hydrophytes, it is suggested that the outline utilized by Hess and Hall (1945) be followed. The examples given are common in the Tennessee River Valley.

*A. Wetland—Typically growing in soils which are saturated with water during a major portion of the growing season (*Echinochloa crus-galli*).

B. Aquatic—Usually growing in soils covered with water during a major portion of the growing season.

1. Emergent—Typically with some of the vegetative parts extending above the water surface.
   a. Erect—Standing upright with relatively firm stems and leaves.
      (1) Leafy—Possessing well-defined leaves (*Saururus cernuus*).
      (2) Naked—Usually lacking well-developed blades, or if blades present, linear and erect (*Eleocharis quadrangulata*).
   b. Flexuous—Having relatively weak stems, or, if firm and erect, with lax leaves (*Leersia hexandra*).
   c. Carpet—With relatively short shoots forming dense, attached mats (*Ludvigia palustris*).

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* The wetland species may be subdivided in the same manner as the emergent, aquatic species.

2. Floating—Typically having the entire plant or some of the vegetative parts floating on the water surface.
   a. Pleuston—Minute plants floating free at the water surface (*Lemna minor*).
   b. Floating mat—Relatively large plants forming a mat at the water surface (*Alternanthera philoxeroides*).
   c. Floating leaf—Attached plants bearing floating leaves (*Nelumbo pentapetala*).
3. Submerged—Typically with the vegetative parts largely submerged (*Najas minor*).

Plant Identification

In view of the fact that the local population (biotype) is considered as the basic unit of autecological research, vouchers should be taken showing the taxonomic and ecological variations of the population. For the identification of the species to be studied, and its associates, the regional manuals should be consulted. They are not listed herein. Three relatively recent manuals of aquatic plants are valuable for Eastern United States (Eyles and Robertson 1944, Fassett 1940, and Muenscher 1944). No attempt is made here to list the considerable number of taxonomic monographs of aquatic genera, but many of them are listed in Fassett (1940) and Muenscher (1944). They should be consulted not only for clarification of taxonomic problems but also as sources of autecological information.

General

Ecology textbooks are of considerable value as references in the study of herbaceous vascular hydrophytes. One of the earliest, and perhaps the best, is that of Coulter, Barnes, and Cowles (1910). In this text more space is given to autecology than in later texts, particularly to roots, stems, leaves, reproduction, dispersal and germination. In addition to the discussion of methods of studying vegetation, Weaver and Clements (1938) present excellent discussions on the hydrosere, and on the adaptation of plants to water. The text by Braun-Blanquet (1932) is noteworthy for its emphasis on phytosociological relationships, and for its discussion of the lifeforms of Raunkiaer. The most recent text (Oosting 1948) includes much of the material in previous textbooks and has one excellent chapter on applied ecology.

The book on water plants (Arber 1920) is still one of the best references on aquatic angiosperms. The first section (114 pages) is concerned with the life histories of aquatic plants, including some carnivores and several halophytes. The remaining sections of the book are given over to the organs of the plants, to the conditions for plant life in water, and to a study of water plants from the phylogenetic standpoint. The Biology of Flowering Plants by Skene (1924) is valuable for the discussions on insectivorous plants, pollination, seed dispersal and seed germination in aquatic plants.

Only a few major references will be given on the relation of environmental factors to aquatic plants. Welch (1935) discusses, in some detail, the nature of fresh water environments, the influence of physical and chemical conditions on the biota, and the role of vascular aquatic plants. Methods of determining the physical, chemical, and biotic conditions of fresh water habitats are described by Welch (1948). The work of Shirley (1945) is important since he discusses the penetration of light into water and means for its measurement. Papers on the germination of seeds of water plants of interest include those of Crocker (1907), Lawrence *et al.* (1947), and Muenscher (1936). The effect of habitat factors on the air space tissue in plants is reviewed by Sifton (1945). One of the most significant papers to the aquatic biologist is that of Hess *et al.* (1946) since it focuses attention on the relation of progression and recession of water levels to seed germination, sprouting, survival, and growth-form of terrestrial, wetland, and aquatic plants. Since the papers of Hitchcock *et al.* (1949, 1950) deal not only with the growth and reproduction but also the practical control by means of 2,4–D of both water hyacinth and alligator weed, they are considered as significant contributions to the study of vascular hydrophytes.

Phenology

Although ecological life history studies are more inclusive than phenological studies, phenology constitutes the major portion of any life history investigation. According to Leopold and Jones (1947) phenology is a horizontal science which transects all ordinary biological professions. In their paper they present much phenological data on many kinds of plants and animals, including marsh plants. The article by Penfound *et al.* (1945) is noteworthy in that it is dedicated almost entirely to vascular hydrophytes. Another interesting feature of the work is the method of recording and portraying phenological data. From the standpoint of phenological interest, it is probable that no species yet studied ranks with the water hyacinth (Penfound and Earle 1948). Perhaps the most significant investigation from the standpoint of portraying the value of phenological data is that of Piemeisel (1951). He showed that the succession from Russian thistle through mustards to downy chess, over a five-year period, could be explained readily by the phenology of the dominant species of each community.

Economic Value

A great deal of autecological information has been collected in the process of attempting to

solve practical problems in herbaceous vascular hydrophytes of economic importance. Considerable information has been collected on the aquatic food plants of man (Chambliss 1922, Fernald and Kinsey 1943, Medsger 1939, Yanovsky 1936). Some data has also been made available on the food plants of migratory waterfowl (McAtee 1939, Martin and Uhler 1939). Other publications (not here listed) deal with food plants of aquatic mammals, and plants of value in fish ponds. Perhaps the greatest quantity of life history data has been collected on those hydrophytes which are inimical to man's welfare. The life history studies on *Achyranthes philoxeroides* (Penfound 1940b) *Dianthera americana* (Penfound 1940a), *Nelumbo lutea* (Hall and Penfound 1944), *Saururus cernuus* (Hall 1940) were undertaken because they promoted the breeding of malarial mosquitoes. The life history study on water hyacinth was initiated because this species caused millions of dollars in damage by : "(1) obstructing navigation, (2) impeding drainage, (3) destroying wildlife resources, (4) reducing out-of-doors recreation, and (5) constituting a hazard to life." The subsequent studies by Hitchcock *et al.* (1949, 1950) on water hyacinth and alligator weed were undertaken for the same reasons. The tremendous damage caused by water hyacinth and alligator weed are described in detail by Lynch *et al.* (1947).

Life History Outlines

In Great Britain the publication of a series of life histories was initiated in the *Journal of Ecology* (British Ecological Society 1941) under the title of the "Biological Flora of the British Isles." A revised schedule for contributors has since been published (British Ecological Society 1947). Since the inauguration of the series, several life histories of herbaceous vascular hydrophytes, common to North America, have been published. These include *Juncus effusus, J. filiformis, J. macer, Polygonum Persicaria, Suaeda maritima,* and *Zostera marina.* Obviously, the series on the "Biological Flora of the British Isles" should be consulted by all workers interested in life history studies of plants. The monumental work of Conway (1936a, 1936b, 1937, 1938a, 1938b, 1940, 1942) on the European sedge *Cladium mariscus* should also be carefully studied.

One of the earliest life history studies in the United States was that of Mattoon (1915) on the southern Cypress. A more recent one on a halophytic swamp tree (red mangrove) was that by Davis (1940). Several life history studies on herbaceous vascular hydrophytes were published before the Ecological Society of America initiated the publication of life history outlines. Included in this series were relatively brief studies on *Achyranthes philoxeroides* (Penfound 1940b), *Dianthera americana* (Penfound 1940a), *Nelumbo lutea* (Hall and Penfound 1944), *Saururus cernuus* (Hall 1940), and *Zizania aquatica* (Chambliss 1922). Two longer articles, one on the greater duckweed, *Spirodela polyrhiza* (Jacobs 1947), the other on water hyacinth, *Piaropus crassipes* (Penfound and Earle 1948), are especially recommended for methodology to the worker on herbaceous aquatic plants.

In the United States, a Committee on Ecological Life Histories was appointed by the president of the Ecological Society of America in 1947. The first outline was written by Fitch (1949) on the ecological life history studies of reptiles. In his discussion of outlines already prepared Lawrence (1950) says that "they have taught us at least two important things: (1) The local population (biotype) of an organism, rather than a single individual, is the true unit of autoecological study, and (2) the life cycle of the organism should be used as the basis for the whole study outline." The first life history study outline on plants is the lengthy one of Pelton (1951) entitled "Outline for ecological life history studies in trees, shrubs, and stem succulents." In it he discusses the value of life history studies, methods to be used, general references, representative studies, and gives a suggested outline. He states that "It will be readily apparent from the following outline that the solving of most of the ecological problems concerning even a single species would require much more time and effort than is ordinarily available to one person." This suggests either (1) that the outline should be shortened or (2) that reasonably complete life history studies should be submitted for publication because of their importance to other workers. Because of the great difference in habitat and the life-form of the plants in the present outline, as compared to the outline of Pelton, much diversity will be noted when the outlines are compared.

Suggested Outline

Classification

Nomenclature.—Valid scientific name; frequently used synonyms; common name, and regions where they are used. Include such other nomenclatural data as may be pertinent.

Description.—Of species and subspecific units, such as varieties, forms, and ecotypes; field recognition characters of seeds, seedlings, and fruits. Taxonomic variability, including chromosome number and hybridity, if possible.

Ecological classification.—Glykophyte or halophyte; wetland or aquatic, with sub-types (see table in text); Raunkiaer life-form; type based on nutrition.

Distribution

Distribution and abundance by regions; past and present range; and reasons for change in range; altitudinal limits.

Habitat

Climate.—Weather station data, and especially microclimatic data. Temperature: seasonal, monthly, extremes, frost-free period. Rainfall: seasonal, monthly variability. Humidity: vapor pressure deficits, especially higher extremes. Light: number of clear days; intensity.

Physiography.—Topography: uplands, hillsides, flood plains, deltas. Types of water bodies where species occurs: Lotic: rivulets, creeks, bayous, rivers; ditches, canals. Lentic: ponds, lakes, river-sloughs, ox-bow lakes; borrow pits, fish ponds, stock ponds, reservoirs.

Substratum.—Water: Depth, seasonal fluctuation, turbidity, pH, salinity, tidal range (if indicated), temperature, light intensity. Soil: Parent material (clay, sand, muck, peat, etc.); soil series and soil profile (if indicated); water level, water content, pH, salinity of soil water (if necessary); and organic matter.

Communities

General vegetation type.—Forests, grasslands, deserts, etc.

Specific communities.—Designate community by major dominants; list all dominants, as determined by quantitative methods; indicate community role of the species under study, together with such qualitative and synthetic data as may be desirable.

Effect of habitat factors

Water level.—Effect of progression and recession on seed germination, sprouting of perennating parts, growth form, and survival.

Salinity.—Effect of a considerable change in salinity on seed germination, size, survival, and community composition.

Pollution.—Result on survival and associated plants.

Temperature.—Effect of exceptionally low or high temperatures on survival.

Mowing.—Effect on growth form and survival.

Fire.—Consequence on survival and community composition.

Plant parasites.—Name of organism; description and assessment of damage.

Animal predators and parasites.—Domestic animals: result of grazing on growth form and survival. Feral animals (muskrats etc.): effect on survival and community composition. Animal parasites: name of organism; damage done.

Morphology and development

Seed germination.—Place and time of germination under natural conditions; germination under laboratory conditions; description of process; range of temperature, moisture, light, and other environmental requirements for germination.

Seedling.—Relative abundance in nature; periodicity in seedling production; gross morphology; longevity and fate of cotyledons; relative rates of growth of root system and shoot system.

Vegetative body.—Indicate whether roots, stems, and leaves are present, and whether in water or in the soil; types of stems (bulbs, corms, rhizomes, stolons, tubers, turions); types of leaves based on relation to water surface, and to season; gross morphology of roots, stems, and leaves; general anatomy, especially details on aerenchyma, chlorenchyma (if present) and vascular tissue; phenology, rate of development; longevity.

Vegetative reproduction.—Gross morphology of structures involved; general anatomy as compared to normal organs; phenology, especially in relation to temperature and water level; longevity of vegetative reproductive structures; comparison of rates of reproduction by vegetative and sexual methods.

Flowers.—Gross morphology of flowers; relative flower production in different habitats; temperature, photoperiod, etc. for initiation of flower buds; phenology, including flower bud initiation, exsertion, anthesis, and pollination; agents of pollination and conditions influencing their effectiveness; pollen quantity, viability, longevity, and germination requirements; degree of self-fertility; evidence of parthenocarpy.

Fruits.—Type of fruit; gross morphology, including numbers of carpels and seeds; phenology, from pollination through maturation to dispersal; proportion of fruits to flowers; quantity of fruit; agents of dispersal; structures involved in dissemination; season of dispersal.

Seed.—Number of seeds per plant; gross morphology of the seed; methods of collecting and storing seeds; length of period of viability; methods of seed germination; environmental requirements for breaking dormancy.

Economic value

Value.—Such as habitats for wildlife; food for man, domestic animals, aquatic mammals, and migratory waterfowl; materials for basketry, etc.

Harm.—Such as its effect on navigation, drainage, recreation, wildlife food plants, and on the breeding of malaria mosquitoes.

Methods of control (of harmful species)

Physical.—Such as removal, recurrent cutting, fire and manipulation of water levels (on artificial water bodies).

Chemical.—List chemicals, formulas, time of application, and results.

. *Biological.*—State degree of natural control (by insects, fish, mammals, etc.) and whether introduction of parasites appears desirable.

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HEMLOCK IN ALABAMA: A SUPPLEMENTARY NOTE

In order to keep the record straight, I would like to point out that most of the localities for hemlock (*Tsuga canadensis*) in Alabama, mapped by Segars, Crawford and Harvill in Ecology for January, 1951 (published in February), are identical with or pretty close to those cited in my report on the trees and shrubs of Alabama in 1928, and others observed by me in later years, some of which have been published and some have not. By taking advantage of better roads than existed in 1928, and automobiles, which were not available in my early years in Alabama (1905–1913), these young men jointly have extended the known distribution of this tree a little way into two or three counties where I had not seen it.

But their map, unlike mine in the publication cited, generalizes the boundaries of the plateau region too much, including with it the geologically younger "basin region," which is not a plateau at all, and in which only one hemlock locality (discovered by me in 1919) is known at present.

They erred in assuming that the first report of *Tsuga* in Alabama was by Charles Mohr in 1901. Dr. Mohr apparently did not know of its occurrence in the state when he contributed a list of trees to Berney's Handbook of Alabama in 1878, or even when he and Dr. Eugene A. Smith published a preliminary check-list of the flora of Alabama, in 1880. But he must have discovered it soon afterwards, for in Prof. C. S. Sargent's report on the trees and forests of the United States, published in 1884, this species is said (p. 207), to have been found in Winston County by Dr. Mohr. A few references to "spruce" in Henry McCalley's first report on the Warrior coal field, in 1886, probably mean hemlock, for that is commonly called "spruce pine" by country people in the southern parts of its range. (The settlement of Spruce Pine in Franklin County takes its name from this tree, as I pointed out in 1906 (pp. 524–525).)

In my first report on the forests of Alabama in 1913, I published a photograph showing the hemlock at Natural Bridge, Winston County, and estimated that it constituted about one per cent of the forest growth of the plateau region. In a revision of that, published in 1943, I used relative abundance instead of percentages, and ranked the *Tsuga* 22nd in abundance among the trees of that region.

In another paper of mine, which Segars *et al.* did not cite, "A depressed outlier of the

Cumberland Plateau in Alabama, and its vegetation," published in 1937, I described one of the most interesting hemlock localities, "The Dismals," in Franklin County, and listed some of the other plants found there. In trying to explain the scarcity of this tree in northeastern Alabama, I suggested in a footnote (p. 17) that it might be due to the excess of evaporation over precipitation there; and Segars *et al.* have since tested that experimentally, as they indicated.

An interesting sidelight on this point, which helps explain the absence of hemlock from Cullman County, except at its extreme western edge, is afforded by some observations in McCalley's report of 1886, previously cited. On pages 83–84, in his description of that county, he says: "Though the larger creeks never go exactly dry, . . . still in a great many sections of the county, during drouthy summers, good water, for both man and beast, becomes very scarce." At that time the county was newly settled and over nine-tenths of its area was still wooded; but now it is nearly half cleared, which tends to intensify both droughts and floods. A friend who has lived on a farm in Cullman County for many years told me a few years ago that he did not know of a single creek in the county that did not stop running in summer. And on a brief visit to him in October, 1951, during a long dry spell, I crossed nearly the whole width of the county from east to west, and saw no running water; only stagnant pools in the creek beds. As the hemlock seems to prefer to grow near permanent streams of cool water, it is not surprising that it should be absent from such a region. In Winston and Marion Counties, where it is still fairly common, the streams are more permanent. In this respect there is some analogy between the hemlock and the redwood of California, which is said to grow naturally only in the fog belt near the coast.

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BIRD ACTIVITY IN THE CONTINUOUS DAYLIGHT OF ARCTIC SUMMER [1]

The continuous daylight of arctic summer is a factor of major ecological importance to animals and plants; few studies have, however, been made under arctic field conditions to determine the relationship between continuous daylight and the activities of birds. This paper reports such observations, which have implications for ecological theories of migration despite the fact that they were limited to relatively few individual birds.

The well known experiments of Rowan (1938) and the later work of others (Bissonnette 1937; Benoit 1936; Wolfson 1945) have established a correlation between the length of daylight and the bird's reproductive status, which appears to initiate its spring migration. A large proportion of the migrations involve flights to high latitudes where the summer days are extremely long; day length could thus have an importance in the ecology of bird migration, in addition to its function as a timing stimulus. Extensive studies have been made of the daily cycle of activity and rest (Szymanski 1914; Wagner 1930; Nice 1943). Such observations have shown that in the laboratory or in the field, in temperate lati-

[1] This study, a contribution from the Department of Zoology, Cornell University, Ithaca, N. Y., was undertaken while engaged in other investigations based at the Arctic Research Laboratory, Point Barrow, Alaska. The support of a research contract between the Office of Naval Research and Cornell University is gratefully acknowledged.

tudes, the sleep-wakefulness cycle is not inherent but controlled by gross alterations in light intensity. A study of the twenty-four hour activity cycles of birds during the continuous daylight of arctic summer is therefore of some interest.

A few observations made at Umiat, Alaska (69° 23′ N. Lat.; 152° 10′ W. Long.) between June 24 and July 2, 1948, are discussed in this paper. During the period covered by the study the sun did not set, its altitude varying between 2½ and 46 degrees. The three species observed were the robin (*Turdus migratorius*), the grey-cheeked thrush (*Hylocichla minima*), and the hoary redpoll (*Acanthus hornemanni*). Of each species one nesting pair and its brood of young

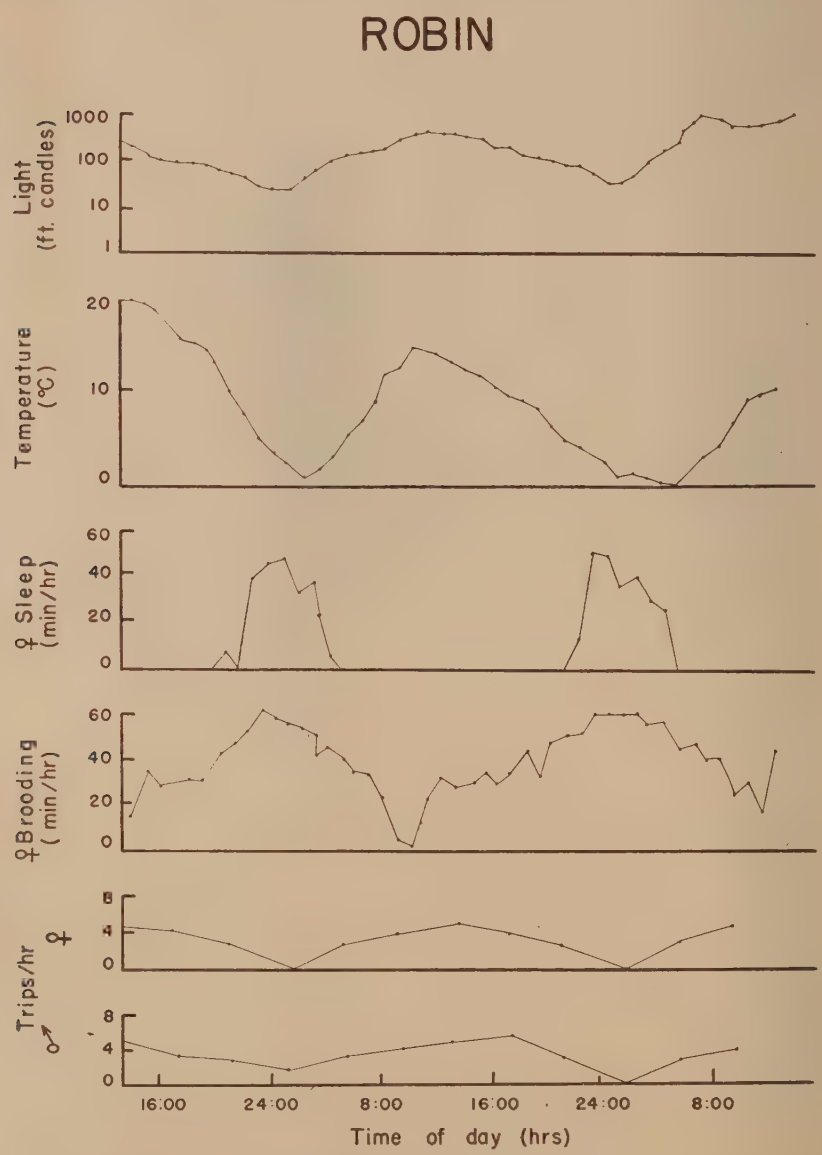

FIG. 1. Summary of 48 hours of continuous observation of a pair of nesting robins at Umiat, Alaska, June 24 and 25, 1948.

were studied, the robins for 48 consecutive hours (June 24 and 25), and the thrushes and redpolls for 24 consecutive hours each (July 2). All of the nests were located in willow thickets and were within 4 feet of the ground. The robin and thrush nests each contained 4 young and that of the redpoll held 5. By semidaily checks the time of hatching of the young robins was determined; at the beginning of the 48-hour watch they were 4 days old. Since the two other nests were found after the young had hatched, their exact ages at the time of our study could not be obtained; estimates might be made from the fact that the redpolls left the nest on July 4 and the thrushes, on July 6.

Nesting birds were chosen to facilitate continual observation of the same individuals. Near each nest a blind was set up, permitting us to watch without disturbing the birds except during changes of observer. At those times the adult bird usually looked up for only a few seconds, and then almost immediately continued what it had been doing before the interruption. The following data were recorded: (1) general behavior (feeding, brooding, cleaning, etc.); (2) air temperature—every half hour; (3) light intensity—every half hour, measured with a de Jur photographic exposure meter pointed vertically upward at approximately 3 feet from the ground (since only the relative light intensity was important, this rather crude method was sufficient).

Activity and Light Intensity

The results of the observations are presented graphically in Figures 1 and 2. It is apparent that the period of sleeping (*i.e.*, inactivity) of the three species occurred at the same time as the minimum light intensity. In the female robin the first sleep was noted when the light intensity dropped below 100 foot-candles and the last period of sleep ended when the light intensity rose above 100 foot-candles again. Different light values at the beginning and end of the sleeping period were observed in the two other species.

Figure 1 also shows for the female robin an apparent correlation between periods of sleep and minimum temperature, a correlation which is nearly as close as that between sleep and light intensity. However, the corresponding curves for the female thrush and female redpoll (Fig. 2) show a similar retriction of sleep to the hours around midnight in a 24-hour period during which the temperature remained nearly constant. The latter observation would tend to exclude temperature as a factor determining the time of sleep. Added evidence for this lack of interdependence may be obtained from the curves for the brooding rhythm, which does appear to be controlled by temperature. The graph for the female robin (Fig. 1) shows increased brooding with decreasing temperature. During a day of nearly constant temperature the female thrush, on the other hand, showed a rather random distribution of brooding time (Fig. 2). A slight increase is evident during the midnight hours as a result of increased sleeping (*e.g.*, between 2:00 and 3:00, the bird was asleep for 50 minutes out of the total brooding time of 53 minutes). The redpoll brooding data present a certain contrast to those of the other species. Here we find that all the brooding is restricted to the sleeping hours; or, perhaps that strictly speaking no brooding occurs, the female simply using the nest as a sleeping place.

A study of bird activity in Lapland (70° N. Lat.) during the summer months has been reported by Palmgren (1935). Observations were made on field trips by stopping for 10 to 15 minutes at a given spot and recording all the birds seen or heard. If no member of a given species was noted at a certain census stop that species was considered inactive (*i.e.*, asleep). From the data Palmgren concluded that the activity rhythm is maintained by an internal 24-hour periodicity, the sleeping period being shifted to occur during the hottest part of the day (1800–2300). Our notes show a lull in singing at approximately the same time (1700–2100). However, the feeding of young birds in the nest, which is certainly a better criterion of activity, showed no decline during the late afternoon. Instead the minimum number of feeding trips occurred between 2300 and 0300.

The governing of the sleep-wakefulness cycle by light requires the bird to differentiate between small differences in light intensity. Doing this through closed eyes would be rather difficult. Our observations showed that the birds slept for stretches of only 10 to 15 minutes, each time opening their eyes before going to sleep again. It is, therefore, reasonable to suppose that the increase in light intensity does not awaken the bird, but that instead the bird notes the increase after awakening and, thereupon, remains awake.

Reduction in the Nestling Period

The migration of birds to high latitudes is a phenomenon of such magnitude that many suggestions as to its survival value have been advanced. One possible advantage is a lengthening of the active period of diurnal birds. Rowan (in press) suggests that "most species summering in the arctic take full advantage of continuous daylight in rearing their families and feed them throughout the 24 hours, so doubtless abbreviating the nestling period. In the case of the larger species this may be a factor of importance in enabling them to make the best use of the brief period of optimum conditions."

Previous studies made in the arctic summer (Palmgren 1935; Baumgartner 1937; Paatela 1938; Tinbergen 1939) show that birds have a

minimum sleeping requirement which, in the species observed, varied from 2 to 5 hours. As can be seen from Figures 1 and 2, our data also show a sleeping period of this magnitude: female robin, average for two periods, 3.7 hours; female redpoll, one period, 3.4 hours; female thrush, one period, 3.3 hours.

The consequences of the lengthened activity period can best be analyzed by studying the behavior of a species nesting both in temperate and arctic latitudes. At Umiat we observed a brood of robins, since this species is common in the United States and it therefore seemed likely that we could find comparable data for temper-

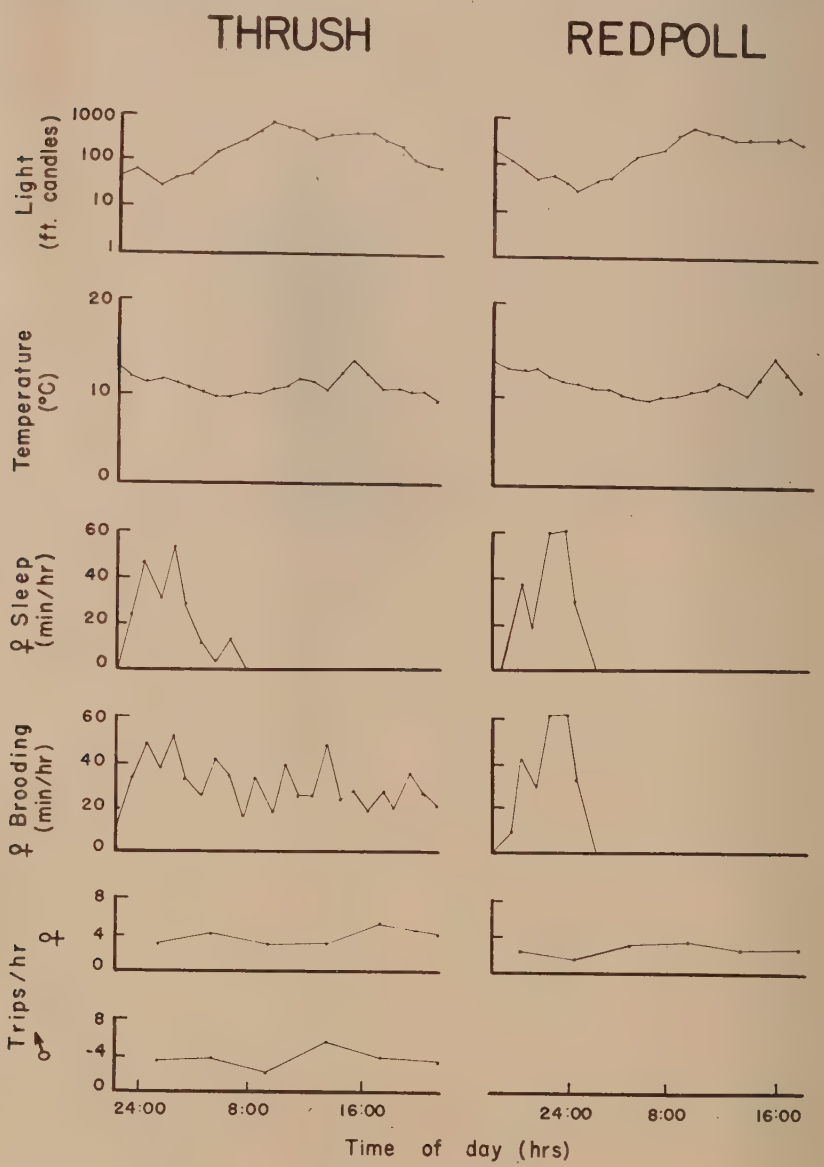

FIG. 2. Summary of 24 hours of continuous observation of nesting grey-cheeked thrush and redpoll at Umiat, Alaska, July 2, 1948.

ate regions. In 85 nests recorded throughout the northern United States (Howe 1898; Tyler 1913; Judson 1915; Allen 1928; Roberts 1932; Hamilton 1935; Schantz 1939; Howell 1942; Nice, personal communication; Speirs, personal communication), the average length of the nestling period was 13.2 days, the minimum being 9 days. It is very probable that the one 9-day period and at least seven out of eight 10-day periods resulted from frequent disturbance of the nesting birds. In contrast to the average nestling period of 13.2 days in the northern United States, the one brood of robins observed at Umiat left the nest 9 days after hatching. The feathering of these young robins indicated that they had developed to the normal fledgling stage and did not leave the nest because of disturbance. The continuous observations from the blind ceased on the 6th day of the nestling period. After that time the nest was checked only once or twice each day in order to determine when the birds would fly. It thus seems unlikely that the 9-day nestling period of these robins was an abnormal one for the latitude of Umiat.

Comparison with a study of nesting robins made at Columbus, Ohio (Schantz 1939) indicates that the more rapid growth and maturation of the arctic birds might be the result of (1) the long periods of daylight, (2) the long periods of active feeding by the parents, or (3) the larger amount of food provided. The young robins at Umiat experienced continuous daylight as opposed to 15 hours per day in Ohio. Studies of young chicks (Heuser, personal communication) show that increasing the length of daylight beyond 13 hours per day does not cause any appreciable increase in growth rate. Insofar as evidence from domestic chickens can be applied to wild birds, this suggests that day length *per se* was not the immediate cause of the rapid growth observed in the arctic.

Our observations during the 4th and 5th day of the nestling period showed that the young robins at Umiat were fed for 21 hours each day, while comparable studies by Schantz in Ohio showed a 16-hour feeding period. As nestlings are usually inactive and frequently asleep when not being fed, the extended feeding period would increase the active time of the young. Chicks (Heywang 1946, 1947; Heuser, personal communication) which were kept in continuous light fed at odd times during the 24-hour day, yet they grew at the same rate as did those fed for only 12 hours each day. Thus prolonged activity, in itself, seems unlikely to have been the agent producing a more rapid rate of growth.

One might expect more rapid growth, other factors being equal, if more food was consumed each day. It was not possible to determine the actual amount of food provided, but it is interesting to compare the number of feeding visits by the adults in the Arctic and temperate latitudes.

TABLE I. *Parental feeding of nestling robins at Umiat, Alaska, compared with data obtained by Schantz (1939) at Columbus, Ohio*

	Trips per hour	Hours of feeding per day	Trips per day	Days in nest	Total feeding trips during the nestling period (estimated)
Umiat, Alaska	6.50	21	137	9	1233
Columbus, Ohio	6.00	16	95.8	14.0	1340

This comparison is made in Table I and is based on the data reported by Schantz and upon the 2 days of continuous observations in Umiat. The table shows that, while the number of trips per hour was approximately the same in the two cases, 21 hours per day of active feeding at Umiat can be estimated to have resulted in 1233 feeding trips during the entire nestling period, if no correction is made for the usual changes in feeding rates. This is not greatly different from the Ohio birds which received 1340 feeding trips during the fledgling period.

Poultry data show that the young do not grow faster if permitted to feed at all times (Heuser, personal communication). However, chicks consumed no more food during 24-hour feeding periods than they did in the normal 12-hour day. This indicates that they are able to obtain all the food which they can metabolize in only 12 hours. In wild, altricial species such as robins different conditions probably exist. The adults may well be unable to provide the young with all the energy they could utilize for growth, even by searching for food continually throughout a 16-hour day (as did the Columbus robins). If feeding is continued for five additional hours per day (as it was at Umiat), more food can be provided, permitting a greater daily total of the metabolic reactions required for the synthesis of tissue components. From this increase in the rate of growth may result the observed shortening of the nestling period.

One factor which has not been considered in the above discussion, though it may be of some importance, is the environmental temperature. During the nestling period the average temperature at Umiat was 14° C. lower than that at Columbus. As birds are at least partly homoiothermic from the second day after hatching, a lower external temperature necessitates a higher expenditure of metabolic energy for the maintainance of body temperature. Evaluation of the importance of the temperature factor in determining food needs and growth rates requires further study.

It is appropriate to point out in closing that a reduction in the nestling period might be ex-

pected to increase appreciably the chance that a young bird will survive to maturity, the nestling period being one of great vulnerability to predators and adverse weather conditions. It seems possible that a very general ecological advantage may accrue to birds that migrate to high latitudes for the breeding season, an increase in the probability of survival of the young which more than offsets the hazards of a long migration. Further quantitative field studies are clearly necessary to ascertain the validity of this concept which is advanced here as only a working hypothesis.

I wish to acknowledge assistance with the observations rendered by D. R. Griffin, R. J. Hock, F. H. Johnson and the encouragement of Dr. Griffin during the preparation of this paper.

Summary and Conclusions

1. The activity cycles of three nesting species were studied briefly in the continuous daylight of arctic summer. The daily periods of rest were more closely correlated with the period of minimum light intensity than with temperature. Together with previous observations of synchronization of song with dawn and dusk in temperature regions, these observations point to the conclusion that the sleep-wakefulness cycle of birds is governed by the environmental light.

2. By comparing a robin nest studied in the arctic with those observed in temperate regions, it was found that the nestling period of the arctic young (9 days) was 4 days shorter than the average for 85 temperate-latitude broods (13.2 days). Further analysis suggests that the decrease in nestling period and the associated rise in the growth rate resulted from the greater number of hours per day during which food was supplied by the parents. The total number of feeding trips for the arctic nest was calculated to be about 1,225, only slightly less than the 1,340 feedings received by a comparable brood in Columbus, Ohio.

3. The observation of a shortened nestling period in one pair of birds indicates that a factor from which migrations derive their survival value is the more rapid growth of young possible in the north.

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The Natural Death of Mice[1]

Characteristically, the best fruits are found on the very tips of branches. Thus, if McCabe and Blanchard are accused of going out on a limb, it may also be argued that their quest made the trip necessary.

This study of three sympatric species of the genus *Peromyscus* (*maniculatus gambelii* Baird, *truei gilberti* Allen, and *californicus californicus* Gambel) culminates in an hypothesis on the environmental control of populations. The authors present good evidence for their conclusions that neither emigration nor ordinary predation is in any way adequate to absorb the considerable surplus of mice that are reared each season. It is equally clear that death-fights do not occur, and that injury through fighting is rare.

From a variety of slight evidence, none of it decisive, the authors conclude that surplus mice, after several mild and harmless rebuffs from occupied shelters, literally die of homelessness.

Evidence is better that, whatever the mechanism of action, the number of shelters is a primary factor determining the population level. Additional support for this is found in the coexistence of the three species, since the strongest ecological differentiation is shown to lie in shelter requirements.

While the authors have constructed a view of what may happen, they do not ask why. The problem shifts from ecology to evolution, but is nonetheless pertinent. Why do young eventually seek a new home? Why does the harmonious living group have its particular maximum size? Why are strangers rebuffed? These are all (presumably) genetic patterns, evolved under particular selective pressures.

In relation to these questions, when considering the role of food as a limiting factor, the authors say: "The distributive instinct . . . probably reflects a long term economy, not the danger of immediate famine." This suggests that food supply, in the past, may have proved an inconstant lover, that the present pattern evolved as a shield against his fickleness. It is possible that food has of necessity been removed as an ecological force to the much more slowly affected hereditary mechanism. This could be approached through a comparative study of group-size, etc. among races of the same species in areas with different minimum food levels.

The authors' hypothesis of environmental control, by itself, favors the Errington school of thought, that predation is largely upon the surplus, that these animals are doomed anyway. And certainly, predation by gopher snakes and other occasional predators during the study could have had little effect on the population size.

But this study records a most remarkable instance of devastating predation. In one of the two areas studied, between the end of March and August, an original well-known population of about seventy-five mice, including all three species, was systematically and completely destroyed by a small group of weasels. The description of this event concludes:

"A picture is derived which may or may not be of general application, of predation not as a continuous toll, more or less within tolerable limits, but as sudden catastrophic descents upon fields which have been left to ripen until worth preying upon."

In a book so richly filled, much can be praised and, inevitably, much can be criticized. To this reviewer, the detailed descriptions of the environment (section I), habitats (II), habit and ecology (III), temperament (VIII), and territorial behavior (IX), portray ambitious planning, tireless execution, and, above all, a remarkable talent for observing what is important, for understanding the peromyscan world. It is seldom that so many observations are correlated and interpreted to such a degree.

Other sections (sexual cycle, III, post-natal development, IV, and molts, VII) are more purely descriptive, and, to the non-peromyscan student, tedious. The accumulation of such detailed information is, of course, important to an understanding of the problem, and many items presented here are later associated with other phases of the investigation.

The remaining sections on growth (VI) and population analysis (X) raise many controversial issues. The authors are to be commended for forging ahead into areas where general agreement is slight, where criticism of whatever they say is a certain result.

A lengthy discussion is devoted to the origin and suitability of the autocatalytic equation:

$$\frac{dx}{dt} = kx(A - x)$$

with the somewhat vague conclusion that, while it is not a satisfactory model of growth, it is about the only one available, and better than nothing.

The last point is debatable. This theory was used for two purposes, to compute the time at

[1] **McCabe, Thomas T., and Barbara D. Blanchard.** 1950. Three species of Peromyscus. Santa Barbara, Calif.: Rood Associates, v + 136 pp., $2.00. [For sale by Barbara D. Blanchard, 1744 Prospect Ave., Santa Barbara, Calif.]

which half the adult weight is reached, and to compare at all ages the observed weights with weights calculated from the best-fit curves.

For the first purpose, adult weights were, after all, observed, and the time of half this weight is easily interpolated from the data. The results are very close to those reached through the use of a questionable theory. In this case a direct estimate of adult weight from data is probably more accurate than an estimate derived through a theory that fits so poorly.

For the second purpose, as the authors say, the comparison does nothing for the theory. But, they add, extenuating circumstances render the discrepancies less objectionable. This can be argued vigorously. These circumstances are good evidence for several phases of growth, and such evidence does not support the use of a single phase growth theory. Unfortunately, an air of apology about these circumstances produces the unintentional impression that it may be the animals that are wrong.

It should also be remembered in these comparisons that sigmoid data and fitted curves must have similar upper plateaus, and also must meet at least once in their lower portions. With such restrictions, and the added restrictions that neither can be vertical or bend backward, the possible range of deviations is not great. Especially in their lower portions, small observed deviations reflect enormous dynamic discrepancies.

In the presence of such abundant interrelation, it is curious that one particular relation was not made. The depression of growth at weaning is severe for *P. maniculatus,* moderate for *P. truei,* and slight for *P. californicus.* Litter sizes decrease in the same order. Actually, the ratios of total litter weights at weaning to average adult weights (rough calculations from the published data) are 2.27, 1.44, and 0.80, respectively.

Much emphasis is placed upon an assumed difference in the growth of these mice from the growth of protozoan and yeast populations. In the latter, growth inhibition is laid entirely to the accumulation of noxious material, a phenomenon not prominent in the growth of higher organisms. The emphasis is such that the authors appear to have missed the many experiments of Pearl, Gause, Richards, Klem, etc. in which growth inhibition among microorganisms is due directly to the depletion of an environmental want.

The section on population analysis is an excellent general discussion, and good reading. It is regrettable that analyses by age and sex are not presented, but the work is already sizable, and such analyses would probably make it unwieldy.

Two results in this analysis are noteworthy. For all three species, in spite of widely different birth-rates, life expectancies, nesting habits, degrees of protection, etc. (and these cannot be appreciated in less than the original text), the percentage of young dying in their first season is the same for all, 81–85%.

Finally, the population maxima for all three species occur in the winter, with minima in the summer. Since this is opposite to the breeding cycle, it may well be that the tolerable group size is greater when the adults are sexually inactive, and that in all seasons the population level is still controlled by the number of shelters.

This review has not attempted to summarize the contents of the study. Whole sections are no more than mentioned. To one person or another, each section will be the richest or most useful part of the analysis. All of it is worth reading to any ecologist.

We are thankful for the terse, distinctive title to a reference that will be appearing in so many bibliographies.

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OF SOCIETIES AND MEN [1]

This is a timely, thought-provoking book. The early pages stress the general evolutionary trend toward complexity in living organisms, and in non-living matter as well. This trend is reversed under restricted conditions as in biotic communities living near their ecological pessimum, in parasitism, or among the individuals composing closely knit societies. Under these conditions evolution is towards simplification and sharper specialization. Among societies there is also a clear tendency towards increased efficiency in social organization.

The author recognizes familial, integrated, and associative societies. Familial societies are the simplest of the three. Integrated societies, such as are highly developed in termites, bees, and ants, have evolved from the family, but are mainly composed of highly specialized, sexually neuter castes, which may differ functionally and structurally from each other. Only a small number of the population retain the ability to reproduce. Associative societies are said to be represented by loose flocks and herds. Such

[1] **Haskins, Caryl P.** 1951. Of societies and men. New York: Norton, xiv + 282 pp.

societies are formed of genetically unrelated individuals. They may be merely fleeting aggregations, but they may attain impressive size and importance.

Human societies are based primarily on the family and on associative groupings. Human culture (perhaps the word *Kultur* will help here) has many resemblances to non-human integrated societies. In both, for example, the majority of individuals are so submerged in the group as to lose much of their individual initiative and their more generalized abilities. Culture societies, Dr. Haskins says, may be regarded as being parasitic, or to have some other less harmful form of symbiotic relationship with the biological aspects of human society. Deep-seated disharmonies exist between biological man and the society of human culture. It is easy to accept the opinion that the resolution of the difficulties in this fundamental conflict presents the greatest social challenge man has ever faced. The author puts the matter even more strongly in saying: "No greater challenge has even been posed to mankind."

Much discussion toward the end of the book concerns similarities between an integrated biological society and a totalitarian state, modern or ancient. Such states have never succeeded for more than a brief period, which, it is true, may have been brilliant. The reasons for the social instability of this form of "Kultur," as put by Dr. Haskins, are decidedly worth reading, but will not be abstracted to be presented out of their full context.

This book is commendably free from obvious mistakes. The author usually screens out anthropomorphisms. It is heartening to find that certain algae, perhaps because they are plants, are said to be "salt-living," whereas, unfortunately, some of the hardier bumble bees are recorded as "snow-loving" and the spiny anteater is described as having a "love of the uplands." My mention of such usage might easily be dismissed as carping, petty criticism were there not so many who impute human emotions to all sorts of non-human animals, to plants, and even to non-living matter as well.

Other small slips occur. For example, the author clearly shows that he knows the significance of castes as developed among social insects, and of the human caste system among Hindus where children are born into the parental caste. It is surprising to find him stating (p. 228) that people concerned with the transmissal of information to others belong to a "specialized caste."

More seriously, this particular reviewer regrets the lack of mention of the beginnings of co-operation, as shown, for example, by the group survival values that characterize many different kinds of animal aggregations.[2] Such aggregations form the basis of Haskins' "associative society." Also, in a different field, I record my own doubts about the assertion (p. 72) that "there is little doubt, for instance, that the young infants of highly civilized peoples are less well developed and more helpless than are the infants of humans at a lower stage of social evolution." How old are "young infants"? Are they new born, or does the statement refer to a somewhat older group after selection has weeded out those least able to survive under primitive conditions? Documentation is needed.

Such defects should not cause prospective readers to question the fundamental soundness of the book. My mention of them may be counterbalanced by citing certain points of excellence. Conspicuous among these is the sound skill used in avoiding the many pitfalls awaiting the unwary use of social analogies between insect and human societies. The essential unity of man with other animals is clearly stated (p. 200), as is the uniqueness of his highly developed power for abstract thinking and ideation.

There is much discussion of the well known idea that the evolution of insect societies in particular, and those of non-primate vertebrates, in large part, depend on genetic mutations, which have a relatively low rate of incidence. Contrariwise, human culture can adjust with spectacular rapidity through the birth and rapid dissemination of ideas.

The culminating conclusion is that human society is not necessarily tied in with the "integrated societies" of non-human animals despite certain close resemblances between such societies and human "Kultur." Totalitarian organization, the author maintains stoutly, is not the inevitable goal of societal evolution of man. The success of societies of termites and of social hymenopterans, in their several ways, does not forecast the future social development of man. "Nature is not so simple" and (p. 251) the totalitarian state is not so much the wave of the future as it is a wave from the past.

The book is attractively printed. There is a short, highly selected bibliography and a helpful index.

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[2] The evidence, which was brought together twenty years ago, is summarized in **Allee, W. C.** 1951. Cooperation among animals, with human implications. N. Y.: Schuman.

Collembola of New York [1]

The Collembola are a group of organisms which are enormously abundant in every conceivable habitat, provided only that moisture is present. Recent studies of soil biology, particularly those of Franz, Gisin, Hammer and others in Europe, have called attention to the important part they play in the formation of humus, together with other minute soil animals. But in spite of their numbers and importance, they are relatively poorly known from the systematic standpoint. Since there has been no general treatment of the North American fauna since Mills' *Collembola of Iowa* in 1934, the appearance of the present monograph is an event of considerable interest.

The format is conservative. The introductory sections deal with the biology, distribution, and economic importance of the Collembola, and with methods of collection and preservation. In the systematic account which makes up the greater part of the volume, the author deals with 41 genera and 160 species; of this number, 4 genera (and one subgenus) and 42 species, besides a number of color forms, are described as new. The 37 plates illustrate the appearance of structural details of most species; 4 plates and the frontispiece, in color, are devoted to life drawings, mostly of Sminthuridae. The book concludes with a glossary, a 40-page bibliography, and an index.

Any survey of the Nearctic Collembola must suffer from the uneven character of previous work on the fauna. While the European Collembola are now fairly well known, the North American species have been treated piecemeal except for Folsom's monographs of several groups; the two most difficult families have never been revised, and only one major revision is less than 20 years old. Furthermore, there is still considerable confusion as to the application of some names, especially in the case of supposedly Holarctic species. If the author has not entirely overcome these handicaps, nevertheless he has made a commendable attempt.

There are, however, a number of serious criticisms to be made. Although the number of forms of Collembola recorded from New York has more than doubled in the last 20 years, and though it is obvious that the present list is not complete, the author makes almost no mention of other species which might be expected to occur. This fact alone reduces the value of the book considerably, since it makes it impossible for the beginner to arrive at even a rough identification of a species unless its genus, at least, is known from New York. This is not merely a theoretical objection; 8 genera not mentioned by Maynard have been found in Connecticut, and representatives of at least 2 of these are abundant in the proper habitat. While it would obviously be difficult to treat these additional forms in any great detail, the inclusion of other North American genera in the keys would have been an addition of the greatest value.

The author states that this book is intended primarily for beginning students. Now, the task of a beginner in identifying unknown animals is never easy; but in this case some golden opportunities to reduce the difficulties have been missed. The keys to families, genera and species are generally satisfactory, but in many cases the author has not taken the trouble to explain, and more important, to illustrate, the key characters. For example: the term "pseudocellus," referring to certain cuticular structures found only in the Onychiuridae and diagnostic of that family, is nowhere explained; the location of the "proximal tubercle" of the third antennal segment, whose structure is used in separating species of *Sminthurinus*, is not stated or figured; and the expression "mucrones lamellate," used in two keys in the family Isotomidae, is not interpreted. Furthermore, although the book is extensively illustrated many of the drawings are devoted to subjects which will be of little assistance to the student, while critical characters are not figured. The colored figures are sometimes (but not always) good, and the principle of figuring the appearance in life is to be commended; but many specimens of Collembola are collected automatically and not studied until after a considerable period in alcohol (in which colors change drastically), and in this case the figures are useless for identification. Even if the material to be studied is fresh, the great color variation of many species makes identification from such figures unreliable. (It is worth noting that in other works also too much reliance has been placed on color characters for separating species, without adequate evidence from morphological differences that the species are really distinct.)

The number of typographical errors is regrettably large. References in the abbreviated bibliography under each taxonomic category frequently do not agree in date with those in the extended bibliography, and a few have evidently been omitted from the latter. In the key to subgenera of *Hypogastrura* the presence of an eversible sac in the antennae is associated with the wrong subgenus. The Entomobryidae are characterized in one family key as having the 4th abdominal segment appreciably longer than

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[1] **Maynard, Elliot A.** 1951. A monograph of the Collembola or springtail insects of New York state. Ithaca: Comstock Publishing Co., Inc., xxii + 339 pp., 37 pls.—frontispiece, 4 text figs. $7.50.

the 3rd; this is not always evident in *Orchesella,* and the reverse is true in *Tomocerus* (included by Maynard in this family). These and other errors are, however, overshadowed by the remarkable figure of a springtail in the introduction showing a "palpus"—a rudimentary structure in the order, which could not possibly occur in the position shown.

It is not the intention of the reviewer to imply that the book is without merit. In a number of respects there is room for considerable improvement, and it suffers by comparison with the monographic studies of Folsom and Stach (though this is almost inevitable, considering the amount of material to be covered and necessary limitations of space). It will, however, be an essential reference for any student of the Collembola, and should be of interest and value to anyone concerned with studies of soil fauna and soil biology.

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New Zealand's Foreign Invaders [1]

This critical, stimulating and well illustrated book, which, incidentally, deals only with the South Island of New Zealand, was written after the author's visit of about two years as a lecturer in geography at Canterbury University College, University of New Zealand. His own investigations and evaluations, which were presented as a doctoral thesis at the University of California, are now fortunately available in this very readable form. It is a brisk description of a deeply appreciated landscape, a striking indigenous flora and fauna, and the effect, in terms of ecology and economy, of an "invasion of men and their floral or faunal camp-followers." That the author is a Canadian, with his roots in another new land, enables him to bring to his subject a sympathetic as well as an experienced judgment on land utilization.

The concept of "invasion" appeals as an extension of work done by New Zealand writers, none of whom contributed his quota with more authority and charm that the late H. Guthrie-Smith, whose *Tutira,* the history of the small world of a single sheep station, remains unique in its approach. Dr. Clark, of course, chooses a wider field, presenting the "revolutionary" regional change which took place over two centuries. He has very effectively pulled together for the first time in a single volume much of the data for the history of the South Island, and some of his emphases and interpretations are new and challenging. The author's decision to confine his work to the South Island seems justified, since the geography and ecology of the two main islands are in the main so different that they are legitimately susceptible of independent treatment, despite the fact that they have always been politically united. Although the diversity of the two islands is well known to the New Zealander, it is worth emphasizing for American readers, many of whom fail even to distinguish clearly between Australia and New Zealand, though 1,200 miles of sea lie between them. Their principal point in common is, in fact, the British ancestry of most of their population.

Dr. Clark's survey is also strongly recommended as a picture of glacial backgrounds, local continentality with treelessness, difficult soils, and finally as a history of early settlement (theocratic in a style reminiscent of 17th-century America) equally outside the experience of North Islanders as of the average American.

In Part I, Dr. Clark sets the stage with a discussion of the primitive habitat. That leads to a consideration of conditions at the time of the coming of the casual visitors who followed Captain Cook toward the close of the 18th century. He stresses the variety of terrain and climate: the great massif of the Southern Alps with living glaciers, and peaks over 10,000 feet high; rocky, semi-arid central Otago; the great Canterbury plain of coalescing gravel fans; wind-swept Southland; and the narrow coastal plain of Westland with its prodigious rainfall and lush forests. An exemplar of these contrasts is the fact that the rainfall at two weather stations lying less than 50 air miles apart differs by as much as 367 inches per year. It is thus difficult to generalize, but Dr. Clark makes the attempt. In discussing Köppen's climatological system he shows that the eastern South Island is characterized by a climate of mild to moderately cold winters; warm but not too hot summers; and limited variability of precipitation from month to month. Indeed, all the stations fall in this *Cfb* classification of Köppen. Comparisons are then made with British Columbia, southern Chile, Tasmania, the Argentine Pampas, western Honshu, western Caucasus, southeast Australia, and the British Islands. Each may fit some part of the South Island, but no great area of it. For the whole island, Dr.

[1] **Clark, Andrew Hill.** 1949. The invasion of New Zealand by people, plants and animals. The South Island. Rutgers University Studies in Geography, No. 1. New Brunswick, New Jersey: Rutgers University Press. $6.00.

Clark might also have suggested the less obvious but broader comparison with North America, excluding arctic and sub-tropical portions. On botanical and physiographic grounds, of course, the comparison with conditions in southern South America is especially well sustained. This range in local conditions is startling in a region that is about the size of Illinois (about 60,000 square miles).

The author's discussions of native ecological conditions are provocative and well-considered, but when he states that grasslands occupy at least 25,000 square miles "in a region well on the moist side of Köppen's grassland boundary, an anomaly to be compared with the grasslands of the Argentine Pampa or the 'prairie peninsula' of North America" he overlooks the theory of Väinö Auer, the Finnish geographer, that increasing winds in southern South America have acclerated the retreat of the forests. The same sequence has held in New Zealand, with changing climate and winds, as has been shown by remains of trees and by podsolized soils on the treeless plains and downs, and confirmed in the south by the fossil-pollen record for postglacial time. Dr. Clark does not entirely overlook the part played by wind, however. He also discusses local pedological types, characterized by "immaturity," thinness, and acidity. He points out deficiencies in calcium, phosphorus and nitrogen, which may be rectified in part by artificial fertilizers.

In Part II, Dr. Clark considers the European invaders, the full story of Maori influence being beyond the scope of his book. He points out that it was Captain Cook's references to seals and his excellent charts that inspired a series of steps by which sealers and others rapidly settled the island. It is parenthetically interesting that the first sealing party, in 1792, killed 4,500 animals in one spot. Here follows a good review of the early sealing and whaling activities, which should be better known to Americans, especially in view of the large number of Yankee ships in the trade—there were 18 in 1837, for example.

Formal settlement began after 1840. Dr. Clark discusses fully the character and origins of the settlers. Repeatedly he insists that the dominant influence was Australian, but even from the facts adduced this seems an overstatement. Though many came via Australia, they were still British cousins once-removed, with the same ultimate background as those who came directly from Britain. His estimate that the latter were composed almost entirely of the "urban poor," lacking in skills and general intelligence, is bound to be challenged. Indeed Dr. Clark himself states that ten years after the founding of the tiny colony of Nelson, some 200 persons were described in contemporary records as "prosperous landholders."

He deplores the lack of farmers among the immigrants, and exceeds a little the bounds of the historical geographer's field, in speculating that a very different attitude toward the land would have obtained had they been mostly of peasant stock, with an "instinct for the conservation of those resources of the countryside which are potentially permanent." In this he seems to ignore the peasant's fear of wet, dark forests, the challenge of resistant soils unlike those of his homeland, lack of capital and of sizable markets until refrigeration was available in 1882, as well as the tremendously difficult terrain of New Zealand, so different from the New World "lands of easier attainment" of which Guthrie-Smith speaks. That a greater leaven of Continental stocks might have resulted in a more varied husbandry has been exemplified, however, in North Auckland, in my opinion, by the enterprise of the more recent Dalmatian immigrants.

Part III is given to the invading animals. The treatment here is lucid and systematic, each important animal being discussed in an interesting manner. Sheep, unsuccessfully introduced by Captain Cook, being the most important, are taken up first. The original settlements, planned in Britain, did not contemplate large-scale sheep farming; the stock came mostly from Australia at a later date. Dr. Clark criticizes the belief that the Island is predestined to sheep raising; he thinks that many cash agricultural crops have been neglected. He traces the course of the sheep industry carefully and notes that by the 1860's it had occupied all the then available land. He considers the subsequent deterioration in grazing land, and urges a closer study of the tussock-grassland problem, not only for its direct effect on the sheep, but especially for its share in the intensification of erosion, so spectacular in many areas. This discussion is very well taken, and should strengthen the hands of conservationists in New Zealand.

Cattle, horses, pigs, dogs, goats, deer, and rabbits are also considered, the problem created by the deer and the rabbits being treated with especial adequacy. Dr. Clark describes the astronomical multiplication of rabbits, and the unique complication created by the conflict between the covert "farming" of rabbits for their skins, and official attempts to eradicate them as pests. Between 1914 and 1939, over ¼ billion skins were exported from the island. Game animals have also become serious pests. These are notably the red deer, described as a very grave menace, the chamois and the thar (these two descended from 19 individuals presented to the Government less than 50 years ago by the Emperor Franz Joseph); the wallaby; and the less numerous wapiti (contributed in 1905 by T. Roosevelt). All these animals help accelerate erosion and compete for fodder with valu-

able domestic animals. Dr. Clark pays a tribute to the efficiency of Government deer-stalkers in attempting to reduce their numbers.

The story of the invading plants is told in Part IV, which is devoted to the types of agriculture now prevailing, and, more briefly, to the species introduced for shelter, etc. Wheat, which displaced potatoes as the principal cash crop in the 1850's, is most thoroughly treated; it becomes an illustration of a pattern of introduction, invention, and spread of particular species and techniques. Wind effect, irrigation (introduced by the gold-diggers), and the valuable breeding work done by the Canterbury geneticists, are considered, as well as peculiarly local practices, more akin to English method than to Australian or North American, in that the grain is treated as an intensively cultivated crop, often in rotation with grasses or roots in mixed farming.

Less space is given to the exotic trees and shrubs, the most prominent of these being the Monterey Pine (*Pinus radiata*), the Monterey cypress (*Cupressus macrocarpa*), and the gorse. The latter, while often a serious pest, is still almost irreplaceable for hedges, which have a very important function in a pastoral economy. The former pair provides two of the best examples in the world "of an expatriated plant which played a very much more important role in an alien habitat than it ever had at home." It is indeed striking to a visitor familiar with California, to see throughout New Zealand hundreds of square miles of these trees grown commercially, in contrast to the very small numbers that persist in the areas in which they are endemic. Dr. Clark fails to note the high incidence of disease in the Monterey Pine in New Zealand, particularly when grown in pure stands, and although he gives timber-cutting figures up to 1940, he does not refer to the tendency of foresters to treat native forests in particular as a single crop.

Numerous photographic illustrations, some outstandingly good, are distributed through the text; several of the oblique aerial shots are most effective. The many special maps are very helpful, though some have suffered from over-reduction. A bibliography comprising about 700 titles is appended, and there is an excellent index. There are few typographical errors and very few obvious errors of fact, the most notable being a misconception concerning dicotyledonous forest trees (p. 29). As to the rôle of the bumble bee in New Zealand, while introductions were made about 1885, as stated by Dr. Clark, it should be pointed out that the late Guthrie-Smith was inclined to think that red clover was fertilized by other agents before that date.

The book is creditable for its method and its systematic presentation of the data. It certainly sheds much light on a part of our world that has proved particularly vulnerable to the invader. As a laboratory report the book should be of much value to ecologists in all parts of the world. Among other things, it corrects the impression that New Zealand is inherently a rich and fertile land. This is in effect a tribute, which might have been more explicitly paid, to the intelligence and adaptability of the new-made farmers of early days. Since it is a record of pre-World War II conditions, a whole decade of development is omitted, as also the answer, in terms of dollars for wool and pelts, to Dr. Clark's criticism of a seemingly unbalanced husbandry.

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The Integument of Arthropods [1]

It is possible that, to some readers, an entire book concerned with the integument of arthropods will indicate a degree of specialization paralleled only by the Arthropoda themselves. Dr. Richards has recently written such a book "designed as a reference work for entomologists and those working in related fields of zoology, chemistry, biochemistry, biology, biophysics, insect physiology, and ecology."

It would indeed be remarkable if scientists from all these fields were equally pleased with the work; unfortunately the ecologist stands to be disappointed. It is especially disappointing to find the ecological aspects of the book touched on so lightly when one considers that the part of an organism in closest contact with its environment is its integument. It is indeed true, as the author states, that the question of ecological niches is complex but this is no legitimate reason for failing to attempt a more thorough discussion of the role the integument plays in adapting the arthropods to the many different environments in which they can be found.

In part because more information is available concerning insects and perhaps in part because

[1] **Richards, A. Glenn.** 1951. The integument of arthropods. 411 pp. Minneapolis: University of Minnesota Press. $6.00.

the author is an entomologist, the arthropod integument is to a large extent synonymous with the insectan integument. The author states his awareness of this situation. But in spite of this it seems incredible that an entire volume designed to interest some chemists, biochemists, and ecologists completely fails to even touch on the biochemical importance of the arthropod integument in relation to the biosphere as a whole. Not one sentence is devoted to the oceanic and fresh water plankton as such and the role their integuments play in the biogeochemical phenomena in the universe. The book seems to lack a comprehensive synthesis of the data reported in a review article-style from some 1800 references.

The book suffers perhaps from the arrangement of its information rather than primarily from the data included. It is divided into three large sections: I. The Chemical Components, Their Combinations, Their Properties; II. The Microanatomy and Development of the Integument; III. The Permeability of the Cuticle. Each of these larger headings is segmented into many small chapters which do not lend themselves to smooth coherent reading. References to a voluminous bibliography are so thoroughly scattered throughout the text that it is often difficult to gain a continuity of thought for this reason. As one example, in the second section, the reader is launched on a chapter concerning the general structure of arthropod integument (which has already been discussed to some extent in the introduction of the book) and then finds himself immediately confronted with the subsequent chapter entitled "Historical and Taxonomic Resumé" before continuing with the following chapter on a discussion of the epicuticle. The information and references set forth in the resumé are of importance but the readability of the book would be enhanced if such material had been relegated to the bibliography and an appendix in the back of the book.

To anyone who has read any literature pertaining to the arthropod integument there is a decided awareness of a need for fewer descriptive terms rather than more. Dr. Richards has failed to perform a service in this regard. He chooses to introduce the term *tectocuticle* for any material poured onto the outer surface of the formed epicuticle and hardening there as a reasonably permanent component. In addition, he objects to the word *endocuticle* as it has been used in entomological literature and suggests that confusion can be circumvented by use of the term *procuticle* for the embryologically original (parent) chitin-protein fraction, retaining the term *endocuticle* for the soft portion of the chitin-protein layer in fully differentiated cuticle. It is the present writer's opinion that confusion will not be lessened by adding such terms to an already "overtermed" situation. We can thank Dr. Richards, however, for carefully footnoting all synonyms of terms which he has used in the text; this may help the invertebrate zoologist through the burdensome terminology. It is gratifying, however, to see the term *sclerotized* well established in the text. This will help, it is hoped, to eliminate the loose statement that any hardened portion of an arthropod integument is chitinized, which suggests the erroneous idea that the chitin component is responsible for the "hardness."

The illustrative diagrams in the text are helpful and clearly reproduced; it is too bad that some of the excellent photomicrographs have suffered somewhat by a lack of glossy paper. Although the handling of the material in the book is a disappointment, there is no doubt that a tremendous quantity of information has been brought together in one place. The bibliography, which includes references to text pages, is a major achievement and for this much many people in the field will be grateful.

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The Acceleration of Evolution [1]

Most of the recent work on evolution is concerned with gene frequency changes in nature or in the laboratory. The genes or genetic systems that are usually examined are either allelic genes showing clear dominance relations or are chromosome segments which segregate in proper Mendelian fashion. A fairly complete analysis of genetic ratios in the population can be made from tests of a captured sample of the population. As a rule complete evaluation of the natural population dynamics would prohibit genetic analysis of the same population (assuming that the natural population dynamics of a species involves interactions between all of the members of that species in at least one stage of their life cycle). That is, an intrinsic uncertainty is introduced into evolutionary studies of natural populations which bears a rough and

[1] **Lerner, Michael I.** 1950. Population genetics and animal improvement. xviii + 342 pp. Cambridge: Cambridge University Press. $5.50.

ready sort of resemblance to the Heisenberg uncertainty.

As a matter of fact, most of the "characteristics" of an animal are not genetic "characters" at all. I do not recognize the members of my family by their eye color or blood type but rather by very general morphological and behavioral traits which have never been analyzed into dichotomies between allelic genes or even into various epistatic, multi-genic or other complications of the Mendelian system. Obviously the Mendelian scheme eventually will be ramified so that a complete morphological picture of an organism will have a statable relation to the genetic composition of the organism in terms of particulate genes or something similar.

The problem now, however, is to describe how heredity works for an organism whose genetics is not so well known as that of the fruit fly or corn or *Neurospora*. Dr. Lerner presents this problem in a clear and fascinating way for the domestic chicken. In modern chicken farming in America the breeder of chicks is confronted with the job of rapidly producing chicks for specific purposes in large quantities. Dr. Lerner gives the impression that the business is highly competitive and that inefficiency or time waste in the production or maintenance of improved strains is punishable by bankruptcy. The chick breeder is therefore in the position of being forced by economic pressure to accelerate evolution to a great degree in order to survive. Darwin, in "The Origin of Species" and elsewhere, emphasized the evolutionary significance of domestic animals. Recently the emphasis has been mainly on non-commercial species, corn being a notable exception.

Many aspects of evolution cannot be satisfactorily examined in nature. More specifically, unless the population dynamics of a species is either known or controlled the significance of gene frequency changes remains highly indefinite. Dr. Lerner presents a case where population dynamics are controlled with great precision by economic pressure, morphological data are abundant, and the allelic inheritance of the elementary genetics course is replaced by a intricate analysis of variance suitable in principle to any population which has been adequately studied from the morphological and population dynamics standpoints. The mathematical exposition is singularly lucid and complete. The fields of statistics, population genetics and genetics in general have recently been characterized by various workers rising in indignation to take issue with somebody about something, even shifting their subject matter slightly so as to be in a more suitable position from which to rise indignantly. It is a pleasure to note that Dr. Lerner isn't angry at anyone. Macromutations don't worry him. Drift effects can come or go. Confidence and fiducial limits likewise. Even the tragic Lysenko problem, which has angered so many eminent men into great loss of dignity, appears only in a footnote. Dr. Lerner has material which is presented well with a minimum of circumlocution.

The first few chapters go into some detail on chicken breeding experiments. It is hoped that this will not discourage those who take the position that a chicken, however noble its lineage, will never possess the *je ne sais quoi* of a small insect or smaller mold. From page 75 on, the book consists of the clearest, most understandable exposition of general population genetics that I have yet encountered. A minimum of previous knowledge is required. Unlike many statistical works, in which the reader doesn't know the plot until he gets to where he came in, the arguments are developed in an extremely well-ordered sequence.

The references to practical poultry breeding scattered through the text, if anything, help in the generality of the book by permitting more convenient visualization of what the same system would look like in nature.

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The Biochemistry of Fish

Under this title the British Biochemical Society has sponsored the publication of a symposium [1] that will be welcomed in diverse fields of biological and biochemical research. The biochemistry of fish is a subject of wide scope with applications that are of the foremost economic importance. Much of the basic research in this field has originated in commercial or government sponsored laboratories. In the last article of the series, entitled "Economic aspects of the utilization of fish," Cutting presents the economic background from which this pressure for fisheries research is derived. The total annual world consumption of fish protein is of the order of one million tons and in many parts of the Orient, and elsewhere, it constitutes

[1] The Biochemistry of Fish. Biochem. Soc. Symposium No. 6, Cambridge Univ. Press, 1951.

a major component, perhaps nearly the sole source of protein in the diet. As summarized by Cutting, the fishing industry is confronted by two major technical problems, preservation and utilization, and by one major biological problem, overfishing. The attention of fisheries biologists is called to this article whose presence is logical, but somewhat unexpected, in a biochemical symposium.

While biochemical knowledge is admittedly indispensable for the solution of technical problems and students of fisheries technology will find the symposium provides a useful framework within which practical problems may be oriented, the contributors, with the exception noted above, have avoided the discussion of practical applications. Emphasis has been placed upon the development of the theoretical picture. This treatment is especially welcome to the ecologist to whom the subject has a twofold appeal. In the first place he is interested in the light that biochemical discoveries may throw upon the evolutionary relationships of animals. In the second place he is concerned with the relationship of the animal to its environment.

The subject of biochemical evolution has received a great deal of attention in recent years and many interesting discoveries have come to light. Pantin [2] has recently discussed the matter in conjunction with morphological problems in a thought-stimulating address to the Zoology Section of the British Association. It may be that the occurrence of a particular substance among a restricted group of animals, as of creatine phosphate in vertebrates and echinoderms, is evidence of an evolutionary relationship but it is equally true, as Pantin points out, that there are a limited number of biochemical processes by which a given result may be achieved and the probability of parallel developments among unrelated forms is correspondingly great. He cites, for example, the frequent occurrence of hemoglobins in diverse unrelated animals and, in view of this, we may well ask whether the appearance of a more unusual respiratory pigment, as of hemerythrin in Brachiopoda, Priapulida, Sipunculida and one polychaet, can be taken as evidence of phylogenetic affinity.

The contributors have paid special attention to this problem of biochemical relationship. When differences exist, and in so far as knowledge is available, each in his turn makes comparison between bony and cartilaginous fishes, and between fishes and higher vertebrates. Less attention is paid to comparison with invertebrates. Following an introduction by Morton, the pace is set by Baldwin in a short but characteristically stimulating first article entitled "Some comparative aspects of the biochemistry of fish." This article opens with a most necessary but unfortunately somewhat old fashioned classification of fishes. It presents the major problems in an interesting and lucid style and provides a unified approach that serves to integrate the disconnected subject matter of the articles that follow. It would be difficult to present such a clear-cut and constructive picture of so complex a subject without falling into an occasional accident of oversimplification. For example, one gains the impression that the kidneys of marine fish are either aglomerular or lack functional glomeruli, but this is somewhat misleading although it is true that the volume of glomeruli per unit area of body surface is much lower in marine than in freshwater species.[3] Again, it is not by any means certain that the formation of urea from ammonia "seems never to have been discovered by invertebrates." The Indian earthworm *Pheretima* has been shown by Bahl [4] to excrete as much urea as ammonia in the urine.

The second problem noted above, that of the biochemical relationship of the animal to its environment, receives a fertile field for investigation among fish. One of the chief issues concerns the adjustments that have been made by fish towards the osmotic pressure of their environment. Baldwin reviews this familiar problem and each of the subsequent contributors pays special attention to differences between marine and freshwater species. The presence of the pressor releasing enzyme renin in the kidneys of freshwater fish and its absence from marine species [5] is not mentioned. Clearly this situation must reflect a part of the water retention mechanism of marine species and one feels that the phenomenon has been rather generally overlooked in discussions of the osmoregulatory adjustments of fishes.

In regard to other environmental factors, food receives some attention, especially in connection with fats and carotenoid pigments, but most of the contributors have little or nothing to say about temperature, illumination, or the effect of hydrostatic pressure. The physiology and biochemistry of deep sea animals must be profoundly influenced by pressure which affects not only the colloid state of protoplasm but also

[2] **Pantin, C. F. A.** 1951. Organic design. Advancement of Sci., **30**.

[3] **Nash, J.** 1931. The number and size of glomeruli in kidneys of fishes, with observations on the morphology of the renal tubules of fishes. Amer. Journ. Anat., **47**: 425–446.

[4] **Bahl, K. N.** 1947. Excretion in Oligochaeta. Biol. Rev., **22**: 109–147.

[5] **Friedman, M., A. Kaplan, and E. Williams.** 1942. Studies concerning the site of renin formation in the kidney. II. Absence of renin in the glomerular kidney of marine fish. Proc. Soc. Exptl. Biol. Med., **50**: 199–202.

governs all chemical reactions in which a gaseous phase is involved. It has been suggested [6] that the poorly developed musculature of deep sea organisms may be correlated with the known facilitation of muscular contraction by increased pressure.

The proteins of fish are treated in a splendid article by Hamoir. Stroma protein, which remains as an insoluble residue after extraction, is low in fish as compared with mammalian muscle. This reflects the lesser development of the connective tissue framework and, one might point out, has little evolutionary significance except as an adjunct to morphological differentiation. However, in this connection, it may be mentioned that there are grounds for believing that fish collagen is structurally different from that of mammals.[7] In respect to the extractable muscle proteins Hamoir has shown that there is a significant qualitative difference between fish and mammalian myogen. Under electrophoresis the fastest component of rabbit myogen migrates two or three times more slowly than the major component of fish. The author states that in this respect frog myogens are apparently related to those of fish, but one would like to have a wider survey. The proteins of lungfishes do not appear to have been investigated and one can only hope that prompt action will preserve some chilled or frozen flesh from the body of the next *Latimeria* that is captured.

The article by Shewan on "The chemistry and metabolism of the nitrogenous extractives in fish" is a useful compilation that contains much valuable information. The author has not neglected the biologically interesting functional aspects of nitrogenous metabolism but one feels an underlying pre-occupation with the economic problems of extractives of the flesh and must turn to Baldwin for an integrated treatment of nitrogenous excretion. There is no mention of guanin, the source of "pearl essence" from the silvery scales of herring and other fish. Shewan is particularly interested in trimethylamine oxide. This substance, which is found in the urine of marine fish and forms up to 30% of their total nitrogenous excretion, is the precursor of trimethylamine which is responsible for the offensive odor of the stale flesh. Dimethylamine is also formed during the staling of marine teleosts but is not produced by elasmobranchs which presumably lack the unknown precursor substance. Freshwater fish, which lack precursors for both these substances, form chiefly ammonia and are much less unpleasant. Freshwater fish are in a chronic state of natural diuresis and excretory ammonia is readily flushed from the system, both through the gills and through the kidneys. In marine forms, on the other hand, there is a physiological shortage of water and Baldwin believes that the production of trimethylamine oxide is a biochemical adaptation to this situation, preventing the accumulation of toxic amounts of ammonia. Whether this be true or not, no such simple explanation offers itself for the peculiar distribution of the dipeptides carnosine and anserine, both frequently lacking in freshwater fishes. Shewan presents his most recent results, in conjunction with a useful summary of the Russian work by Yudaev who used partition chromatography to identify the dipeptides. Baldwin, on the other hand, quotes the older work of Clifford to show that the distribution of carnosine is best understood on a classificatory basis.

The article by Lovern on "The chemistry and metabolism of fats in fish" is of exceptional interest, as might indeed be expected from the years of careful research which this investigator has devoted to the subject. The fats of terrestrial vertebrates are composed almost exclusively of triglycerides of the familiar C 16 and C 18 fatty acids. The fats of fish are far more complex containing straight chain, even number fatty acids ranging in length from C 12 to C 26 or C 28. A high proportion of these fatty acids are of the unsaturated type, containing from one to as many as six ethylene bonds. The significance of this complexity remains obscure. The role of temperature has often been discussed and there have been several recent contributions to this subject.[8, 9, 10] It is evident that one must expect to find lower melting point fats in the bodies of poikilotherms, especially if they inhabit cold water, but research indicates that the subject is far more complex than this. Salinity affects the composition of the fat, freshwater species tend to have short chain fatty acids and the plankton crustacea reflect the same difference that is

[6] **Pickford, G. E.** 1946. *Vampyroteuthis infernalis* Chun. An archaic dibranchiate cephalopod. I. Natural history and distribution. Dana—Report No. 29 (pp. 13–14).

[7] **Gustavson, K. H.** 1950. The effect of anionic detergents on collagens of mammals and teleostei. Acta Chem. Scand., **4**: 1171–1184.

[8] **Hunter, J. G.** 1948. The change in the degree of unsaturation of body fats during acclimation of goldfish (*Carassius auratus*) to high temperature. M.A. Thesis, Univ. Brit. Columbia (unpublished).

[9] **Hoar, W. S., and J. E. C. Dorchester.** 1949. The effect of dietary fat on the heat tolerance of goldfish. Canad. Journ. Res., **27D**: 85–91.

[10] **Wilber, S. G., and M. del Pomo.** 1949. Comparative study of lipids in whole carcasses of arctic and non-arctic fish. Proc. Soc. Exptl. Biol. Med., **72**: 418–420.

observed in the fishes. There is a body of evidence to show that the type of fat ingested affects the composition of the depot fat, nevertheless fish can convert ingested fat both in respect to degree of saturation and to chain length. On reading this article one feels that, out of the mass of data presented and analysed, there is little of evolutionary significance; the emphasis is all on environmental correlations.

Goodwin's article on "Carotenoids in fish" begins by stating that there are no differences between marine and freshwater species. However, in a final section he points out that as marine fish can synthesize vitamin A 1 from beta carotene, so freshwater species can synthesize vitamin A 2, the precursor of their special retinal pigment. Beta carotene occurs in the ovary, rarely in the liver. Apart from this there are three carotenoid pigments, lutein, taraxanthin and astaxanthin, which may be found in fishes. Lutein and taraxanthin are usually mutually exclusive, one finds either the one or the other, but their distribution appears to have no classificatory significance and even closely related forms may thus differ in the nature of their xanthophore pigment. Astaxanthin, the pigment of the erythrophores of some species, may occur with either of the orange-yellow pigments. Goodwin's article contains a welcome review of the theory, due to Hartmann and coworkers, that astaxanthin is a fertilization hormone.

The bile salts of fish, reviewed by Haslewood, appear to offer much promise for future work. Elasmobranchs have a C 27 alcohol, scymnol, conjugated with sulfate, and in this respect resemble frogs and toads. Teleosts, on the other hand, appear to be "modern," with a C 24 acid, cholic acid, combined with taurine. Chenodeoxycholic acid may also be present and there is some evidence of other bile acids. The possible occurrence of cholic acid in some elasmobranchs requires further investigation.

In conclusion one may say that in a symposium of this sort, however good it may be, there is bound to be both repetition and omission. In the latter category one feels the need of an article which might have been entitled "Vitamins, enzymes and hormones in fish." The enzymes associated with muscle are ably reviewed by Hamoir who pays special attention to the problem of thiaminase which is so rarely present in marine species of fish. But nowhere in the symposium can one find a discussion of the digestive enzymes of fish although some of these have been partially purified [11, 12, 13] or even isolated in crystalline form [14, 15]. Fish proteinases are known to be different from those of mammals; crystalline salmon pepsin, for example, does not attack the specific synthetic substrates that are split by swine, sheep, and chicken pepsin.[16]

There is no discussion of fish hemoglobin nor of the serum proteins, although it is of evolutionary importance to recall the special peculiarities of cyclostome blood. Alone among vertebrates the respiratory pigment of the lamprey contains a single heme,[17, 18, 19] and ultracentrifuge studies [20] have revealed important peculiarities of the serum proteins. In general the cyclostomes have received rather scant biochemical attention but perhaps one good result of the present plague of lampreys in the Great Lakes may be an increased knowledge of all aspects of their physiology.

Goodwin has an interesting discussion on the source of vitamin A but otherwise the whole subject of vitamins and hormones is neglected. Fish insulin is known to be identical with that from mammalian sources [21] but there are physiological reasons for suspecting that fish thyro-

[11] **Boos, C. S.** 1943. An investigation of the pancreatic proteinase of the shark *Carcharias obscurus*. Catholic Univ. Amer., Contrib. Biol. Lab., **45**: 1–56.

[12] **Lucey, M. R.** 1943. A study of pancreatic lipase of shark and swine by continuous potentiometric titration at constant pH. Catholic Univ. Amer., Contrib. Biol. Lab., **43**: 1–55.

[13] **Sprissler, G. P.** 1942. An investigation of the proteinase of the gastric mucosa of the shark. Catholic Univ. Amer., Contrib. Biol. Lab., **42**: 1–55.

[14] **Norris, E. R., and D. W. Elam.** 1940. Preparation and properties of crystalline salmon pepsin. Journ. Biol. Chem., **134**: 443–454.

[15] **Norris, E. R., and J. C. Mathies.** 1947. The gastric proteinase of the yellow fin tuna (*Neothunnus macropterus*). Fed. Proc., **6**: 281.

[16] **Fruton, J. S., and M. Bergmann.** 1940. The specificity of salmon pepsin. Journ. Biol. Chem., **136**: 559–560.

[17] **Svedberg, T., and A. Hedenius.** 1934. The sedimentation constants of the respiratory proteins. Biol. Bull., **66**: 191–223.

[18] **Roche, J., and M. Fontaine.** 1940. Le pigment respiratoire de la lamproie marine (*Petromyzon marinus* L.). Ann. Inst. Oceanogr., **20**: 77–86.

[19] **Wald, G., and A. Riggs.** 1951. The hemoglobin of the sea lamprey *Petromyzon marinus*. Journ. Gen. Physiol., **35**: 45–53.

[20] **Svedberg, T., and K. Andersson.** 1938. Ultracentrifugal examination of serum from the lower classes of vertebrates. Nature, **142**: 147.

[21] **Jensen, H., O. Wintersteiner and E. M. K. Geiling.** 1929. Studies on crystalline insulin from fish islets (cod and pollock) and from pig's pancreas. The activity of crystalline insulin and further remarks on its preparation. Journ. Pharmac. Exptl. Therap., **36**: 115–128.

globulin may be dissimilar to that of higher vertebrates [22] although the ratio of thyroxin iodine to total iodine is the same in shark and cattle thyroid.[23]

A concluding comment by Wormall calls attention to our lack of knowledge of fish serology. The Serological Museum of Rutgers University is sponsoring research in this field,[24, 25] and in California, according to a note in the *New York Times* for Aug. 21, 1951, Dr. J. E. Cushing is studying the "typing" of fish blood as a clue to migration.

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[22] **Smith, D. C., and S. A. Matthews.** 1948. Parrot fish thyroid extract and its effect upon oxygen consumption in the fish, Bathystoma. Amer. Journ. Physiol., **153**: 215–221.

[23] **Dey, B. B., P. S. Krishnan, and M. Giriraj.** 1945. The iodine content of the thyroid gland of sharks. Journ. Sci. Industr. Res., **4**: 244–246.

[24] **Gemeroy, D. G.** 1943. On the relationship of some common fishes as determined by the precipitin reaction. Zoologica (N. Y.), **28**: 109–123.

[25] **Gemeroy, D. G., and H. L. Baier.** 1950. Recent advances in the collection of serum from marine animals. Serol. Mus. Bull., **5**: 3–4.

Huntington, Ellsworth. 1951. *Principles of human geography.* Sixth edition, revised by Earl B. Shaw. xviii + 805 pp. New York: John Wiley; London: Chapman & Hall. $6.25. Ecologists will not expect to find new generalizations about human ecology in this revision of a standard textbook. They should be interested, however, in whether their students are being well grounded in the fundamentals of geography, for no branch of applied ecology, from agriculture to air conditioning, can ignore those fundamentals, whereas "pure" ecology is equally dependent on geographic relationships. It is pleasant to record that this is a textbook of the highest quality.

Geography as a discipline suffers from diffuseness, of outlook as well as of content, and the massiveness of this volume is perhaps its only serious defect. Despite the restriction to "human" geography, there appear to be more parts and chapters than are really necessary. Perhaps that is a consequence of aiming a textbook at both high-school and college students. At any rate, the reference material is ample, stimulating problems are provided, and the illustrations range from "well chosen" to downright enthralling. The literary style is about what one expects in a textbook, but otherwise the authors and the publishers have spared no effort and missed no technical tricks in making this an outstandingly attractive and interesting introduction to a perpetually fascinating subject. *E. S. Deevey.*

Peters, H. S., and T. D. Burleigh. 1951. *Birds of Newfoundland.* xix + 431 pp. 32 colored plates and 40 figures by R. T. Peterson. St. John's: Department of Natural Resources, Province of Newfoundland. $6.00. (Available from Houghton Mifflin Company, Boston.) This work, published under the sponsorship of the government of Newfoundland, is ". . . intended to aid the people of Newfoundland in identifying the birds of that Island and to provide information concerning these birds." Without doubt the book will admirably accomplish its purpose but to those who had hoped for new information it will be a great disappointment. It is little more than a compilation of previous work, with a smattering of original observations, graced by a number of attractive plates.

The first fifty pages of the book are concerned with discussions of life zones, previous work in Newfoundland, classification, conservation and what might have been a highly useful discussion of avian biology. A commendable attempt was made to indicate that ornithology consists of more than the field identification of birds, but it is unfortunate that the authors presented so much of the material in an opinionated manner that fails to convey to the novice bird student that all is not known about the subject.

The remainder of the book covers the more than 200 species found in Newfoundland. Under each species are given the local names, a brief description of the species, and very general notes on field marks, nests and eggs, range, its status in Newfoundland, habits, etc. Considerable emphasis has been placed on the "common" names with subspecies stressed, even though no other race occurs in the region. This leads to rather cumbersome combinations. Several novel innovations have been introduced as, for example, *Aegolius funereus richardsoni,* which in North America is commonly known as Richardson's Owl but here appears as the American Tengmalm's Owl, or *Seiurus noveboracensis uliginosus,* a race of the Northern Water-thrush, which is called the Newfoundland Small-billed Water-thrush. There seems little need to discard the more common names in favor of these.

The reader will be annoyed by the deficiency of references to the original literature in the text, although one section of the book contains several hundred titles under the heading of "Literature Cited and Selected Bibliography."

The plates are up to Peterson's usual standards but the unfortunate addition of an extra digit on the Arctic Three-toed Woodpecker (Plate 19) will probably harass the artist for many years.

Although the ecologist will find little of use to him in this book, the attractive plates, the comparatively low cost, and the very easily read text will appeal to many amateurs and increase interest in the birds of Newfoundland. *Raymond A. Paynter, Jr.*

Anderson, E. 1949. *Introgressive hybridization.* ix + 109 pp. New York: John Wiley and Sons. $3.00. This slim volume, the first of the Wiley Biological Research Series, is a lucid exposition of the methods for studying hybridization in the field. Many of the methods of graphic analysis are here presented for the first time, although some of the results of their use have been published by Anderson. These analyses are used as examples. The illustrative material is almost entirely botanical. This book should stimulate interest in the analysis of hybrid populations of animals, as such studies have been neglected. *J. L. Brooks.*